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A COMPENDIUM

OF

GENERAL BOTANY.

BY

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TRANSLATED BY

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With 171 Illustrations.

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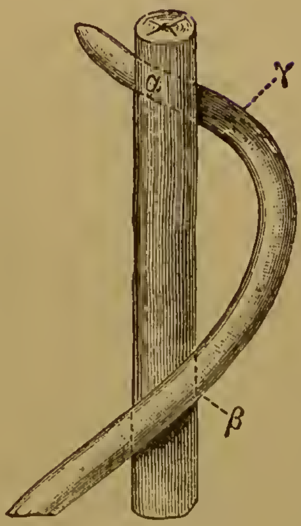

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PREFACE.

In a compendium of botany intended for *high schools* it is permissible to introduce subject-matter which would be objectionable in a text-book of elementary instruction. Free use has been made of such privileges. It is assumed that the pupil has a general knowledge of chemistry, of physics, of the proper use of scientific terminology, and has the ability to estimate the value of hypotheses and undecided problems. From the consideration of the latter the disciple of our science will soon recognize the peculiar difference between layman and scientist. The layman looks upon many phenomena in plant-life as being quite clear and easy of explanation. The scientist, however, can demonstrate that we know but very little concerning these same phenomena. It must also be borne in mind that scientific progress depends upon the recognition of the present limits of our knowledge.

Nearly every branch of science is more or less merged into *general cosmology*. It is therefore expected that every scientist should attempt to explain this relation. We find that the various authors have a tendency to call the reader's attention to the important (in the author's opinion) phases of cosmological relationship. Even of this privilege I have made use.

Incidentally I will make the following observation: The greater portion of physiology is intimately associated with anatomy. In accordance with this we find that the newer development of botanical science considers the question, What for? of prime importance when investigating plant-structures (anatomical-physiological tendency of Schwendener's school).

In the special as well as in the general treatment of the subject-matter I have frequently made use of the works of Nägeli, Sachs, Pfeffer, de Bary, Frank, Göbel, and Warming; more especially those of Schwendener and his pupils (Haberlandt among others). To this I have added the knowledge obtained through a long scientific association with my honored instructor, Professor Schwendener. The illustrations are added with the kind permission of various authors. For all this I express my sincerest gratitude.

MAX WESTERMAIER.

FREISING, October 1893.

TRANSLATOR'S PREFACE.

In presenting this translation it is perhaps well to offer a few explanatory statements.

The book is just what the title implies, a *compendium* of *general* botany. Its great value as a text-book lies in the thoroughly *logical* and *scientific* treatment of the subject-matter. The necessarily condensed retrospect of the science of botany is well supplemented by the copious, well-chosen references to standard authorities.

I have endeavored throughout to adhere as closely as possible to the author's form, style, and concept of the science of botany. The arrangement and treatment of the subject-matter are the same as in the original. In fact I have endeavored to make it a translation in the true sense of the word. I have, however, added some foot-notes. A few are explanatory; others serve to indicate differences of opinion. Although it is difficult to make a good translation of the finer shades of meaning peculiar to a language, yet I sincerely hope I have met with fair success in such an attempt.

Finally, I desire to express my grateful obligations to Dr. N. L. Britton, who made the final corrections of the proof for the first half of the translation. I am also greatly indebted to my wife, who has kindly aided me in correcting the manuscript and in reading the proof.

ALBERT SCHNEIDER.

COLUMBIA COLLEGE, July 1895.

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COMPENDIUM OF GENERAL BOTANY.

DIVISIONS OF SCIENTIFIC BOTANY AND GENERAL CONSIDERATIONS.

THE two domains of plant study are MORPHOLOGY and PHYSIOLOGY.

Morphology treats of the *substance* of the vegetable kingdom. *Physiology* treats of the *forces* or energies bound up with the plant-substance or which manifest themselves with it. Plant-functions, as we know them in the light of morphology and physiology, are not only proper adjustments to the environment, but above all fulfill the requirements of plant-life and are therefore life-functions. To define the term *life*, even only in its application to the plant kingdom, is impossible. Science can, however, proceed more and more into the *order of things*, to know more clearly the properties of matter and the harmonious manifestations of force. In spite of this progress we cannot approach any nearer the solution of the "life-problem." Processes of a chemical and physical nature are the most that we are able to see in this *order* of things and this knowledge distinguishes the scientist from the layman who sees the order less clearly. The earnest investigator who has concluded to believe by faith finds the answer to the "why" of this order in the words "wonder of creation." To the one who is not so inclined this "why" becomes a darkness which grows denser in proportion as he sees more clearly the order in which chemical and physical processes are combined as they are in plant-*life*. Life *manifests* itself in certain chemical and physical processes, and in so far as physics and chemistry are concerned in life-processes there is a "physics and chemistry of plant-life." Plant-physiology may be designated by the expression "physics and chemistry of plant-life," but always in the sense that the exactness of the knowledge of life-manifestations adds nothing to the causal mechanical explanation of "life" itself.

To *morphology* in the above sense belongs the description of the form, size, arrangement, and outer and inner numerical relations of the plant-body; therefore *anatomy* is a part of morphology in the wider sense. Usually, however, anatomy (inner form-relations) is distinguished from *morphology in a narrower sense* (outer form-relations). Thus limited, morphology forms one of the fundamental principles underlying our present *system* of classification.

Let us now return to the *two* main divisions of our science. A few examples will make clear to the novice how morphology may be distinguished from physiology, but that a complete and comprehensive knowledge of the plant necessitates a *combination* of the two.

When an investigation has for its purpose the explanation of the cause of development of the *woody cell-wall*, then it concerns itself with a *function*, in this special case a function of nutrition; this is therefore physiology. If one makes a microscopic comparison of one wood with another and seeks to find the similarities or dissimilarities of the tissues, then no functions are involved and the study is morphology (anatomical morphology). If one seeks to find the relation of anatomical differences to the environment (as a rule this relation is considered from a teleological standpoint), then we must of necessity concern ourselves with physiological processes. If we seek after the conditions which cause plants to turn green, then the study is purely physiological: we are solely concerned with energies. If, with the aid of the highest magnifications, the finest structure of chromoplastids (chlorophyll bodies) is studied in order to describe them more correctly, we are concerned only with morphology. Development, for example, embryology, belongs to morphology. To study, describe, and represent graphically, the successive stages of embryonic development lies wholly in the domain of morphology. If one, however, makes a study of the wall of the ovum in order to determine experimentally what *forces* eventually determine the position of the first septum, then we are again in the domain of physiology. If a minute description is given of the various cell-forms found in the stem, where, for example, the thick-walled cells occur, the form of the thickenings, etc., then we are concerned with morphology. If, however, one seeks for the significance of this or that cellorm in the service of plant-*life*, then again we are concerned with force effect which is bound to a specially constituted plant-substance and is therefore physiology.

Throughout the arrangement of this book a strong effort s made to adhere as strictly as possible to the combination of uch methods of investigation as have just been indicated. However, some attention must be given to the didactic uses of the book. ue regard shall be given to a proper summarizing. In its entirety ve have adopted that disposition of subject-matter which Schwen-ENER has so efficiently tested and found useful in the academic ourse of study. His arrangement is as follows:

I. *The cell.*
II. *Tissues.*
    A. Structure of tissues and simple organs.
    B. Differentiation of tissues (physiological anatomy of simple organs).
III. *Systems of organs.*
IV. *Reproduction.*
V. *General chemistry and physics of plant-life.*
VI. *System of plant classification.*

PART I.

THE CELL.

I. INTRODUCTION.

The organisms which we designate as plants, though variable, have one thing in common: they are either single *cells* or *cell-complexes.* There is, so to speak, only one element in plants, and that is the *cell.* Every plant consists of at least one cell.

Omitting for the present the embryonic conditions of the *cell.* it may be defined as, for the most part, a microscopic *closed vesicle* consisting of *wall* or *covering* and *contents* (large cells, as those of *Gossypium* species, 6 cm. long; medium-sized cells, as those of elder-pith). We must distinguish between younger and older stages of the cell. At first an apparently homogeneous, mucous, tenacious substance—*plasm*, *protoplasm*—fills the entire cell-cavity (*lumen*) and is enclosed by the cell-wall (*membrane*). The components of the cell-contents designated by the collective noun "plasm" are *albuminoid* substances and hence contain besides carbon, hydrogen, oxygen, also nitrogen, sulphur, and sometimes phosphorus. Its mucous consistency is noticeable by its spontaneous escape from openings of the cell-wall (swarm-spore formation of algæ, etc.). Gradually there appear differentiations in the apparently homogeneous plasm. Spherical particles filled with a watery substance—*vacuoles*[1]—are distinguishable from the more dense contents; the latter, the true plasm, are of different kinds, not homogeneous, as a superficial examination would indicate. The *plasmic utricle*, which is of special importance, shall irst claim our attention. The water-bearing cavities (vacuoles) inrease more and more in size and subsequently come in contact and ecome flattened by mutual pressure. Finally they are separated nly by thin plasmic membranes and threads; when these break the acuoles flow together to form one. The plasm then lines the inner urface of the cell-wall as a nembrane which is usually ery thin, but which is ever absent from the livng cell. This membrane s called the *primordial tricle* or *plasmic utricle.*)n account of its frequently mmeasurable thinness it is nvisible as long as it is n contact with the cell-vall. If by artificial means he plasmic utricle can be aused to separate from the vall by contraction, then his is looked upon as givng evidence that it was a *iving* cell. (Compare Fig. .)

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[1] According to more recent investigations (WENT) the "vacuoles" originate from pre-existing ones. (The conclusions of this investigator are generally conceded to be erroneous.—Trans.)

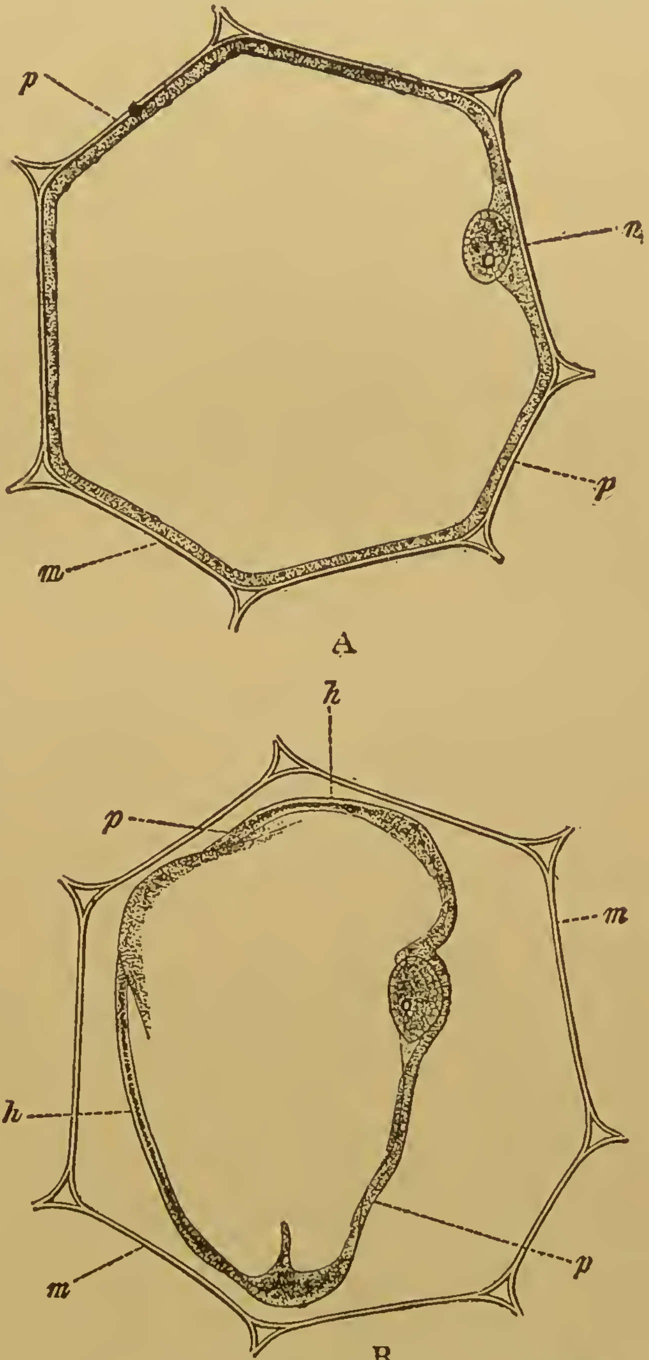

Fig. 1.—Young parenchyma-cell of *Zea Mays.* *A*, normal; *B*, plasmolyced. *m*, membrane; *p* and *h*, protoplasmic utricle; *n*, nucleus; *s*, cell-lumen with sap. (After Frank.)

The cell-wall and the lasmic utricle, the two overings of the cell conents, differ (1) chemically, that the primordial utrile being a part of the plasm an albuminoid substance, hile the cell-wall belongs the group of carbohyrates and contains therere C, H, and O, the latter the proportion to form ater (H_2O); (2) physically, in that the cell-wall is highly elastic ith but little extensibility, while the plasmic utricle is very exnsible and only slightly elastic. To this must be added a second hysical difference, that of *diosmosis.* The physical differences are of such great importance that they will be more fully treated in Chapter II.

The formation of the plasmic utricle is, as has been indicated, not the only differentiation product of the plasm. In the entire plasmic body one can distinguish a fundamental substance ("cytoplasm"—from χύτος, cavity, cell) and inclusions formed within this *fundamental substance.* These inclusions are of two kinds, (A) living and (B) dead. The plasmic utricle and threads constitute the cytoplasm. The *living* inclusions are the *nucleus*, the *chromatophores*, and the *fertilizing elements*, made up chiefly of nuclear substance and having a reproductive function. Of the *dead* substances formed from the plasmic body the most important are *protein-grains*, *protein-crystals*, *starch-grains*, *crystals* (of fat, salts, organic acids, etc.), *oil-globules*, and *tannin*. The term "chromatophores" includes three substances: chlorophyll bodies, color-granules, and colorless starch-builders. These bodies are considered collectively because they are either the bearers of color-substances or are formed out of such to be again converted into chromoplastids. (STRASBURGER, SCHIMPER.)

The space not occupied by the above-mentioned solid constituents is filled with a watery fluid, the *cell-sap* (sometimes having color-substances in solution).

It is important to bear in mind that within the living cell gas accumulates only in very small quantities. No bubbles are ever rapidly formed.

The reaction of *cytoplasm* is usually alkaline or neutral. In the *living* cell, cytoplasm has the property of reducing very dilute alkaline silver-nitrate solutions. (LÖW and BOKORNI.) In the cytoplasm an outer hyaline layer (*hyaloplasm*) and a more granular internal layer (*polioplasm*) may be noticed. According to REINKE the plasmodia of *Aethelium septicum* contain 73% of water, and judging from the mucous nature of other forms of cytoplasm we may conclude that they also contain a high percentage of water. To plasm in general, especially its important structures, as nucleus and chloroplastids, one no longer ascribes homogeneity.[1] Careful microscopic examinations reveal a *reticulated* (spongy) *structure* of plasm. (SCHMITZ, BÜTSCHLI, and others.)

All life-processes of the cell take place within the plasm. A cell without plasm does not grow, does not take in food, does not live. There is no mechanics of plasm; cell-life is still wrapt in obscurity. Direct observation shows that plasm gives rise to the cell-wall, as in the case of *Stigeoclonium*.[1] The plasmic utricle contracts, escapes from the opening in the cell-wall, and in time surrounds itself with a new wall. To trace a phenomenon back to plasm is as a rule the present limit of our ability.

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[1] I would especially recommend WIESNER'S Elementarstructur, 1892.—Trans.

II. PRIMORDIAL UTRICLE AND CELL-WALL IN THEIR MUTUAL RELATIONSHIP.

TURGOR. PLASMOLYSIS.

The primordial utricle is usually of immeasurable thinness. In order to represent it in a figure such cells or portions of cells are selected in which it is of perceptible thickness as it lies in contact with the cell-wall. As a rule it can be made visible only by causing it to separate from the cell-wall either through causes inherent in the cell itself or by *artificial means*. When this plasmic contraction is artificially induced it is recognized as "plasmolysis." The phenomenon of plasmolysis can be explained only from the inherently different properties of the cell-wall and primordial utricle. It is at once evident that the endosmotic properties of the bladder of an animal filled with a solution of some salt cannot be compared with a living cell. It can only be compared with a dead cell-wall.

If a living cell with cell-sap (ex., hair-cell of petal of *Tradescantia*) of a given concentration is placed in distilled water, then the endosmotic flow of water through cell-wall and primordial utricle into the cell is greater than the outflow of cell-fluid. The endosmotic substances within the cell attract the water, which therefore increases the cell volume. The limit of this increase is determined by the cell-wall because it is less extensible than the primordial utricle, although much more elastic. (Elasticity is that force which replaces displaced molecules. It is very great in the cell-wall and very small in the plasmic utricle.) The cell-wall is therefore a hindrance to the excessive expansion of the primordial utricle. Action induces reaction: the cell-sap which exerts a given pressure upon the cell-wall in turn receives an equal pressure. This mutual pressure of cell-sap upon cell-wall and cell-wall upon cell-sap is called

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[1] Studied by NÄGELI.

"*Turgor.*"[1] Sometimes the cell-wall cannot resist the expansive force of the continually expanding primordial utricle, and as a result the wall will rupture, which indeed sometimes happens in nature. If the utricle is not ruptured at the same time, then it may expand to the limit of resistance and finally rupture.

Let us now suppose an inverse case. Let there be a more highly concentrated solution outside and a relatively more dilute cell-sap within the cell. In this case more fluid passes outward, and as a result the entire cell decreases somewhat in size. Here again becomes manifest the difference in behavior of the two cell-coverings, the plasmic membrane and the dead membrane (cell-wall). The cell-wall contracts a given amount, corresponding to its previous expansion. If the wall is very delicate and the action of the solution very sudden, it may be thrown into folds and may finally collapse. As a rule the action of the external solution is sufficiently slow and the cell-wall of sufficient thickness to escape such deformity, in which case the *primordial utricle is removed from the inner cell-wall,* corresponding to the decrease in volume of its interior. This continues and the space between cell-wall and utricle is filled by the solution from the outside and the inner cell solution. This behavior of the primordial utricle with certain concentrated salt solutions is also shown with certain dilute poisonous liquids, as for example iodine solution, and dilute acids. A longer or shorter exposure will kill the cell. The primordial utricle no longer permits all substances in aqueous solution to pass alike. In the case of plasmolysis this fact becomes known by the great contraction of the primordial utricle, so that it collects as a lump either in the centre or near one side of the cell. If, conversely, cells filled with cell-sap, as for example those of beet-root, are placed in pure water, for hours no sugar will pass into the surrounding liquid, although the membrane in itself certainly allows sugar to pass. Upon this impermeability of the living utricle to certain substances rests the possibility of producing within the cell a high hydrostatic pressure, amounting at times to ten or more atmospheres.[2] (PFEFFER's investigations.) The apparent *elective* choice which plants show in regard to the appropriation of food-substances does not depend upon this plasmic impermeability. This term should be used with caution. There certainly is no subjective choice. Whether a given substance is taken up by the plant depends upon whether it is of *use* or not. The unequal utilization of certain substances by different plants depends upon inherent peculiarities of the plants. For example, of two plants growing in the same soil one will take up much and the other little silica (SiO_2), the one much and the other little calcium carbonate, and deposit it in the cell-walls. The above-mentioned behavior of plasm toward poisonous solutions is quite different and might in a certain sense justify the term choice. It is, however, strictly speaking only the reaction of the living plasm to chemical stimuli.

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[1] Owing to the lack of a corresponding English noun I have retained the original.—Trans.

[2] This subject will again be referred to under Water-movements and Tissue-tension.

For the investigations concerning plasmolysis we are indebted to several authors, Nägeli, Pringsheim, Pfeffer, and more recently Hugo de Vries. To the last-mentioned investigator we are indebted for a very important treatise entitled the "Analysis of the Turgor Force."[1] This analysis was made by determining the so-called "isotonic coefficients." I will select only the following statements from the work of de Vries. The *weakest* solution (expressed in gram-molecules, not per cents) of potassium nitrate (KNO_3) which is just capable of inducing plasmolysis within a cell has the same attractive force for water as any other diosmotic combination, as for example oxalic acid, which is sufficiently diluted to just induce plasmolysis. Such concentrations of equal tension are said to be "isotonic." Chemically related substances have the same coefficient. If the isotonic coefficient of KNO_3 is 3, then it is also 3 for NaCl, KCl, in fact for all *alkaline salts with one atom of the metal in a molecule.* For organic compounds such as malic acid, citric acid, acetic acid, the coefficient is 2, as has been determined by actual experiment. For alkaline salts with two univalent acid radicles, as for example $MgCl_2$, $CaCl_2$, it is 4, etc. De Vries further determined chemically the various combinations in the cell-sap and then found the turgor force exerted by each (sum-total).

The relation between turgor and growth will be referred to in the chapter on "Physiology of Growth."

Before entering upon the discussion of the cell-contents it should be noted that the contracting primordial utricle carries with it all the solid constituents of the cell-contents; also that the primorthat nuclei sometimes rupture during sudden artificially induced plasmolysis.

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[1] Analyse der Turgorkraft, Pringsheim's Jahrbücher, XIV (1884).

III. CELL-CONTENTS.

Tedious microscopic examinations of the cell-contents aided by staining methods have recently brought to light a series of facts and form-relations. But so far no conclusions of considerable importance have resulted therefrom. The partially compiled and partially original communications of A. ZIMMERMANN[1] are especially suited to give a comprehensive view of the work done and our present knowledge of the subject. The most important results of the above-mentioned investigations were obtained by the study of the nucleus and the amyloplastids (starch-builders). STRASBURGER, GUIGNARD, ROSEN, SCHMITZ, KLEBS, ZACHARIAS, HABERLANDT, and others have made special studies of the nucleus, while SCHIMPER has devoted much attention to the amyloplastids.

For the sake of clearness it is no doubt permissible to select from a subsequent chapter a few statements concerning cell-formation before taking up the cell-inclusions.

In general cells originate in two ways: by *division* and by *free cell-formation*. In the first case the form of the mother-cell and the position of the septum determines the form of the daughter-cells. In the second case the daughter-cells are approximately spherical and float freely within the contents of the mother-cell. In both cases the cells grow after they have formed. Deposits may be made in all parts of the cell-wall—uniform surface growth—or only at one portion—apical growth of cell. In the latter case the cell will gradually become more and more elongated.

A. LIVING INCLUSIONS OF THE CYTOPLASM.

(a) *Nucleus.*

1. The nucleus is a more dense plasmic structure and is usually present in all cells, though it is difficult to prove its existence in the fungi. Some very large cells, as for example of *Caulerpa* (an alga) which are often a foot or more in length, contain many nuclei; long bast-cells contain several nuclei. The majority of cells, hence those

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[1] Die Morphologie und Physiologie der Pflanzenzelle. Breslau, 1887. Beiträge zur Morphologie und Physiologie der Pflanzenzelle, I. II. III. Tübingen, 1890, 1891, 1893.

of microscopic size, contain only one nucleus. A similarity in the form of the nucleus to that of the cell is not noticeable. In the younger cells it is approximately spherical; after the period of cell-growth it becomes more ellipsoidal. It often lies near the cell-wall imbedded in the plasm, sometimes it is suspended in the cell-lumen by means of plasmic threads. To demonstrate the presence of the nucleus it is advisable to kill the cell with concentrated picric acid, which "fixes" the plasm, and subsequently to stain it red with hæmatoxylin solution or green with methyl green.

The nucleus, again, contains one or more nucleoli.[1] The nucleus (exclusiue of nucleoli) contains besides true albuminous substances a characteristic compound or group of compounds also albuminoid in nature, namely, the phosphorus-bearing nuclein. It swells in a 10% solution of NaCl and is dissolved in a solution of potassium hydrate which distinguishes it from true albumen.

As a rule the nucleus is located in that portion of the cell where growth (growth in thickness or surface of cell-wall) is the most active or where it continues the longest. Usually the nucleus assumes a definite position only in the undeveloped cell, later the position is indefinite. Rarely it may assume a definite position for a second time.

From the foregoing statements it is to be supposed that the nucleus is of special significance in the processes of cell-growth. *What* rôle it really does play and what functions it subsequently subserves is still a question. The observations made by Klebs upon artificially-divided cells are of special interest. It was observed that only that portion of the cytoplasm which contained the nucleus is capable of growing in length and surrounding itself with a membrane, while the function of the remainder is assimilation only.

The difference between cell-division and free cell-formation is, according to our present knowledge of nuclear behavior, not so great as was formerly taught. During each cell-division and in general during each *free* cell-formation there is a *nuclear division.* The so-called *indirect* nuclear division occurs most frequently, and is connected with extensive changes in the nuclear substance. The details of this mode of nuclear division have been made known by Strasburger, Flemming, Guignard, and Heuser.

I will not enter into a comprehensive description of indirect nuclear division or "karyokinesis," but will limit myself to the explanation of the accompanying figures. One usually distinguishes a "chromatin" and an "achromatin" nuclear figure. The former is distinguished by the readiness with which the nuclein is colored by various stains, the latter is composed of the slightly staining portions of the nuclear substance. In the illustrations the chromatic figure is indicated by heavy dark lines, the achromatin figure by light lines (*E*, *F*, *J*, *M*). Roux assumes hypothetically that the purpose of karyokinesis is to transmit hereditary peculiarities by means of the dividing decisive substances (chromatin threads or bands). How-

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[1] There are often denser portions noticeable within the nucleoli.—Trans.

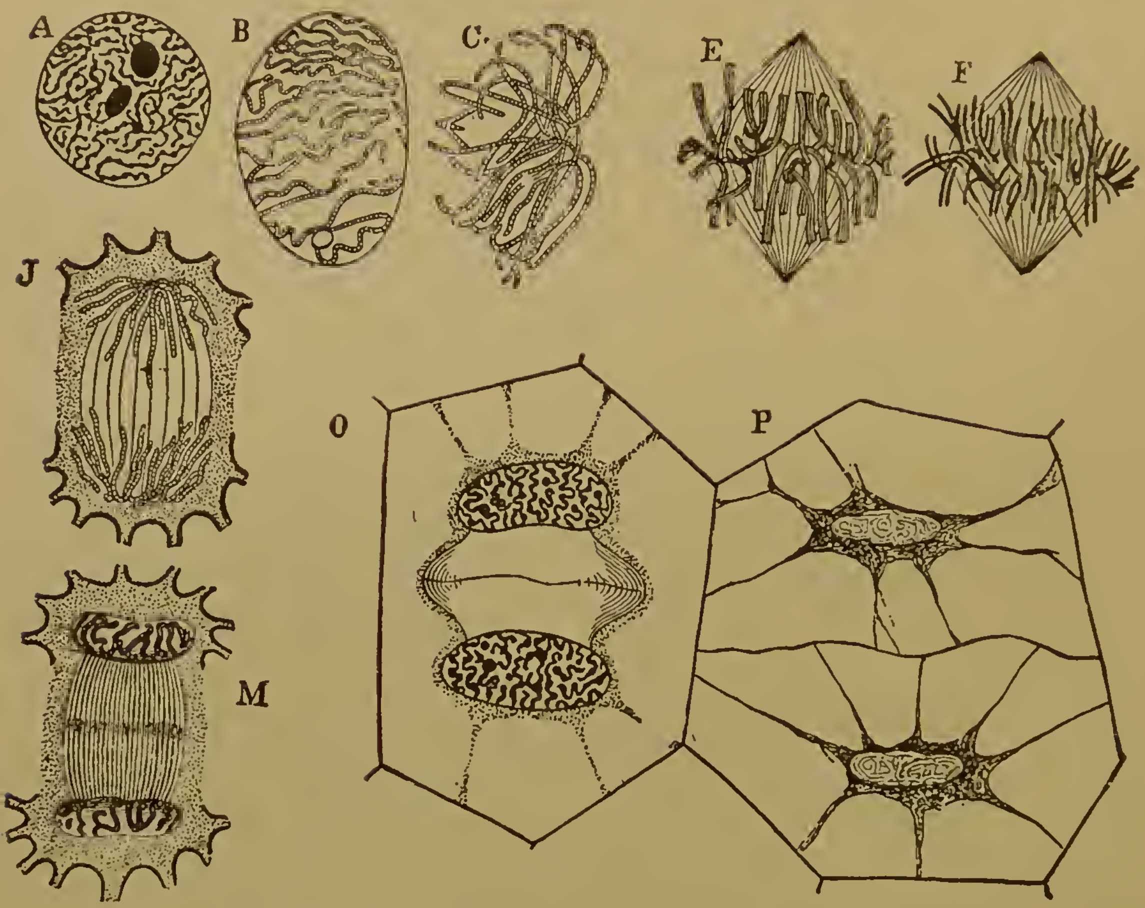

FIG. 2.—Successive stages of nuclear division.[1] (After Strasburger.)

In *A* an irregularly wound thread is formed from the nuclear network (spirem, Knäuel). In *B* and *C* are seen the "chromatin-granules" resulting from the breaking up of the chromatin. At *E* and *F* a certain arrangement and *longitudinal division* of chromatin-threads takes place. Somewhat previous to this the *achromatin* nuclear figure makes its appearance (delicate lines in *E* and *F*). The two halves of the chromatin-threads move along the fine achromatin lines in opposite directions to the poles (*J*) and form the "spirem" (Knäuel) stage of the daughter-cells (*M*, *O*). Out of the spirem is formed the network, nucleoli appear, also a nuclear membrane, and the daughter-nuclei are complete. When a septum is to be formed a cellulose plate forms between the two daughter-nuclei at the points where the thickenings occur on the nuclear spindle; otherwise the nuclear spindle (achromatin-figure) disappears with the thickenings.

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[1] In connection with indirect nuclear division should also be mentioned the recently discovered and studied "centrospheres" or "directive spheres," small spherical bodies, normally two in number, lying just outside of the nucleus, which also undergo considerable change in position during nuclear division.—Trans.

ever, the same uncertainty still surrounds "heredity" as it does the "idioplasm" of Nägeli.

A process directly opposite to that of nuclear division is the *union* of *nuclei.* This process evidently plays a part, though unexplained, in reproduction, in the fertilization of one cell by another. (See chapter on Reproduction.)

(*b*) *Chlorophyll Grains*, *Chromoplastids*, *Leucoplastids.*

These three structures are, as has been indicated, included under the name chromatophores. A discussion of chlorophyll bodies will lead to the discussion of chromoplastids and leucoplastids.

In all *chlorophyll bodies* there is a green coloring matter, *chlorophyll.* It is intimately associated with the highly important function of carbon assimilation, which will be discussed later. Even in the carbon-assimilating plants of a red-brown or blue-green color (as for example red and brown marine algæ) it is assumed that they contain active chlorophyll, but that it is hidden by some other coloring matter. Among vascular plants there are also numerous instances where the chlorophyll-bearing cells are colored red by the cell-sap. Among phanerogams, vascular cryptogams, and mosses the chlorophyll bodies are *disk-shaped*, though usually spoken of as "chlorophyll grains." These disks lie with the flat

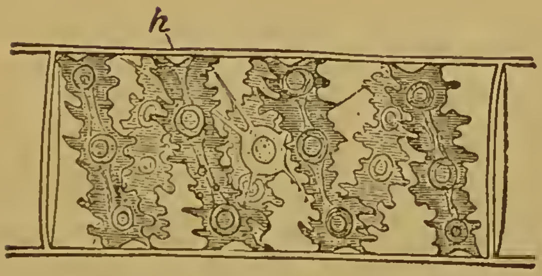

FIG. 3. (After Sachs.)

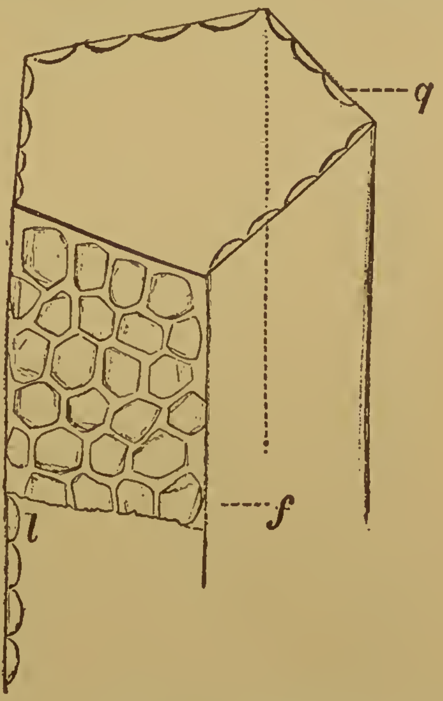

FIG. 4.—A portion of prismatic cell with lateral chlorophyll - bodies (schematic).

Optical cross-section at *q*; surface view at *f*; optical longitudinal section at *l*.

surface in contact with the thin primordial utricle, thus having the appearance of being in contact with the cell-wall. Among the algæ the chlorophyll bodies may assume the form of *disks*, *bands*, *plates*, or even radiate like a star. In the *Palmellaceæ* (unicellular algæ) the plasmic body, with the exception of the nucleus and hyaloplasm, is colored green. Among the *Phycochromaceæ* (nucleus wanting) there are no differentiated chlorophyll bodies, but the entire plasmic body is homogeneously colored. Spiral chlorophyll bands are seen in *Spirogyra* (Fig. 3), which also has a nucleus suspended in plasmic threads. A portion of a palisade cell (typical assimilating cell of leaf) with chlorophyll bodies is shown in Fig. 4.

Origin of Chlorophyll Bodies.—Chlorophyll bodies often result from direct division. When a chlorophyll-bearing algal cell divides, each daughter-cell receives a part of the chlorophyll, which part continues to increase by growth or division. Young cells in growing areas (apical areas), as for example in the stems of the higher plants, are supplied with a colorless plasm. It is, however, supposed that these cells contain *leucoplastids*, that is *colorless plasmic bodies which may become green on exposure to sunlight.* No doubt the unicellular embryo contains besides nuclear substance also leucoplast substance, and that there is no development *de novo* of either. Both multiply by division. (Schmitz, Schimper, Meyer.) Under certain conditions *leucoplastids* may be converted into chromoplastids, that is non-chlorophyllous coloring bodies. The first of the two important functions (chlorophyll and starch-forming) of leucoplastids has thus only been touched upon. The leucoplastids are also found in tissues devoid of chlorophyll where starch is formed from pre-existing dissolved products of assimilation, as for example in the potato-tuber. These leucoplastids are called "starch-builders" (Schimper) because they develop starch-grains; either on their periphery or within the interior, similar to chloroplastids with the aid of sunlight; but with the important difference that in the latter case the raw materials are CO_2 and H_2O, while in the case of the starch-builders the starch-grain is formed from dissolved starch, or more generally from assimilated food-substances brought from the green cells. The nature of the starch-builder can be explained best in connection with a chlorophyll-grain (Fig. 5, cell *Z*). The chlorophyll-bodies are represented as producing starch-bodies on the periphery at *c′* and within the interior at *c″*. The

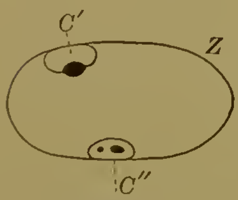

Fig. 5.

starch-builder (amyloplastid) is *colorless* and forms starch within or upon it in the manner described.

Leucoplastids are very unstable and easily destroyed, hence not readily demonstrable. In the living cell they must be rapidly acted upon by certain reagents, as for example an aqueous iodine solution. Their form is usually spherical, sometimes elongated or spindle shaped owing to the presence of crystalloids.

The *chromoplastids* form the coloring substances of the variously colored flower and fruit parts. One fact is to be remembered, namely, that the red, blue, and violet colors are often due to substances in solution in the cell-sap. Yellow chromoplastids, for example, are found in the cells of the beet. The form of the chromoplastids varies; they may be spheroidal, disk-like, radiate, or elongated.

At this point it is well to make a few statements concerning (1) metamorphosis; (2) the destruction of chlorophyll (SACHS, G. KRAUS).

1. Chlorophyll bodies may be converted into red chromoplastids, thus causing the red coloring of fruits. This has been demonstrated in many instances. The red detected in the winter coloration of *evergreen leaves* (*Conifers*, *Buxus*) disappears in the spring. In these plants the chlorophyll bodies are not entirely destroyed; they lose only a portion of the green coloring matter, while carmine-red drops appear which again disappear in the early spring.

2. On the other hand the autumn coloration of falling leaves, the yellowness of straw, the change in color of dying plants or parts of plants, is due to the destruction of the chlorophyll. The entire plasm and the chlorophyll bodies of falling leaves enter into dissolution and the important constituents pass into the more persistent parts. A yellow coloring matter (xanthophyll) remains in the leaves in the form of small granules. In the case of the red coloring of falling leaves there is in addition to these yellow granules a red cell-sap (grape).

There is still another plasmic structure to be mentioned which the more delicate microscopic manipulations have brought to our notice, namely, the so-called "starch or amylum clusters" or "pyrenoids." In composition they resemble most nearly the nucleoli or nucleus. They are found almost exclusively among the algæ, where they usually occúr *within* the chlorophyll bodies, evidently constituting centers of starch-formation. As a rule they are enveloped by numerous starch-granules, hence the name.

Those organized plasmic masses which represent the fertilizing elements in reproduction will be referred to in the chapter on Reproduction. Before passing to the consideration of the dead inclusions of cytoplasm we will mention a few special plasmic structures whose significance is, in part, not well understood.

1. *Cilia* (Wimpern, flagella) of swarm-spores and spermatozoa serve as organs of movement. Their number and manner of attachment vary greatly (one or two, covering the body entirely, or only partly). The cilia of spermatozoa originate in the cytoplasm; they are not nuclein.

2. The so-called *eye-spot* (red or red-brown) in swarm-spores of algæ had already been noticed by earlier authors. Morphologically it belongs to the chromatophores (KLEBS). It is said to be very sensitive to mechanical pressure and to certain alkaloids. Its function is unknown.

3. The iridescent plasmic plates in the superficial cells of various marine algæ probably serve to protect the chromatophores from intense light (discovered by BERTHOLD).

4. In root-tubercles of Leguminosæ there are constantly found certain proteid bodies resembling bacteria, called bacteroids[1] (*Brunchorst*). They eventually serve the purpose of converting nitrogen-bearing organic compounds into albuminoid substances.

We will now turn our attention to the dead inclusions of cytoplasm.

B. DEAD INCLUSIONS OF CYTOPLASM.

Dead inclusions as distinct from "plasmatic" inclusions play only a passive rôle in plant chemistry. This, however, does not make their physiological significance any less important. In the discussion of many of these structures I shall adhere in general to A. ZIMMERMANN'S[2] treatment of them: this also will hold true of my treatment of the general morphology of the cell.

In mass and importance *starch-grains* stand first. Almost equal to them in importance but of less frequent occurrence are the *aleuron-grains* (gluten), including the protein-crystalloids. To these must be added fat-crystals, solid coloring substances, and mineral excretions, especially in the form of crystals.

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[1] These bacteroids are now generally admitted to be true bacteria belonging to the Schizomycetes. Their development has been observed in culture media.—Trans.

[2] Die Morph. und Phys. der Pflanzenzelle. Breslau, 1887.

The two first named substances (starch-grains and aleuron-grains) are represented highly magnified in the figures shown below. Fig. 6 represents both starch and aleuron as they occur in seeds of *Pisum sativum* (pea). Fig. 7 represents starch-grains from a potato-tuber.

(*a*) *Starch.*

In 1858 NÄGELI made known the results of his investigations relative to the growth of substances capable of imbibition (as opposed to crystals), especially starch-grains and cell-membranes. The chief conclusion arrived at is that *growth of starch-grains and cell-walls is by intussusception* and not by apposition as in crystals. (The cell-wall will be discussed later.)

Stratification of starch-grains is not the result of deposits of successive layers so that the outermost layer is the youngest. On the contrary the layers are the result of *internal* processes of growth and differentiation: there is nothing superimposed upon the outermost layer, which really existed from the very beginning. The cause of the stratification is to be found in the alternating layers of greater and lesser percentage of water (therefore more and less dense layers); since excessive evaporation or absorption of water causes them to become less distinct. Optically, by the aid of the polarization microscope, it can be shown that starch-grains react as though composed of uniaxial crystals. Under the crossed Nicol prisms

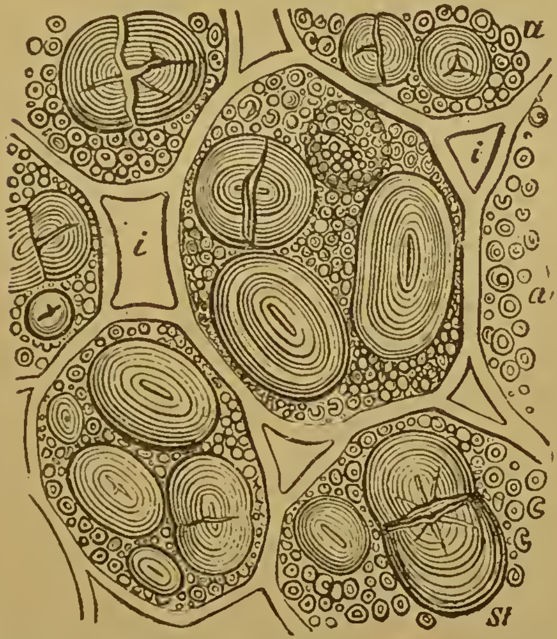

FIG. 6.—Cells from the seed of *Pisum sativum*.
(× 800.) (After Sachs.)

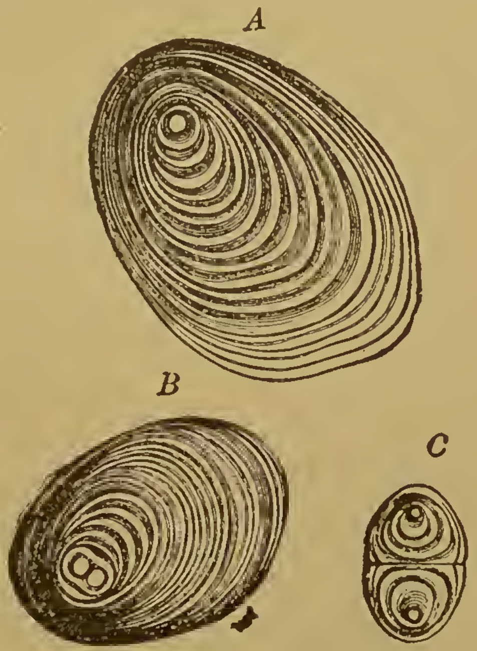

FIG. 7.
A, simple starch-grain of potato-tuber; *B*, partial compound; *C*, compound. (× 800.) (After Sachs.)

there appears a bright rectangular cross whose arms form an angle of 45° with the polarization plane of the nicols.

Of Nägeli's arguments in favor of growth by intussusception I will now mention the particular one which, according to SCHIMPER'S[1] more recent investigations, can no longer be maintained. Fig. 7 shows two "compound" starch-grains. According to Nägeli these are usually the result of differentiations within the starch-grain (usually nuclear division) and only exceptionally through the fusion of two individual grains. Schimper has demonstrated for a large number of plants that subsequent fusion of individual starch-grains does take place.

The theory of *intussusception*, whose acceptance is favored by reasons to be given below, teaches that starch-substance in solution (for example glucose), hence starch-molecules and water-molecules, passes into the interior of the growing starch-grain, and that from this material new molecular layers are formed and the size and density of already existing molecular masses are increased.[2] The increase in density of the starch-substance depends upon the increase in size of the molecules which grow by apposition, similar to crystals.

The following evidence and considerations speak in favor of the intussusception theory: 1. In the earliest stage the starch-grain consists of a uniformly dense substance: such is the nature of the very small grains; however, as soon as they increase in size, there is formed a softer, more watery (not denser) nucleus or central layer. 2. The outermost layer of the growing starch-grain is always more dense. 3. The demonstrated presence of the internal tensions of the starch-grain also harmonizes with Nägeli's theory. In the outer layer of the young, still firm, spherical starch-grain there originates and exists a positive tension; in the interior a negative tension. The outer layer receives the first and greatest food-supply, and as a result it is first to increase in area. When the negative pressure in the interior mass (plus the effort to deposit food-material) has reached a certain height, the soft nucleus (hilum) is formed. Similar processes take place in the outer dense layer; this is repeated again and again. It may be stated here that Nägeli believes the *causes* for these molecular changes, namely, the attraction of starch-particles for each other and for water, to be certain molecular forces "*whose nature is unknown*."[1] Nägeli has probably advanced as far as it is possible to go in this field of investigation. He has reached the given forces inherent in the smallest particles of matter.

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[1] Botanische Zeitung, 1880, 1881.

[2] NÄGELI, Stärkekörner, S. 291.

The above does not compel us to accept the intussusception theory. However, it cannot be denied that the evidence given explains certain phenomena more satisfactorily than the apposition theory.

It would be very desirable to establish a definite reliable life-history of a starch-grain; to observe directly its development from beginning to end, for example in a culture medium. We arrive at the conclusion of "younger" and "older" stages of starch development in an abstract way by describing as many stages or conditions as we happen to observe. Conclusions as to age are then indirectly reached according to the size of the starch-grain under examination and by other considerations.

The opinion of ARTHUR MEYER[2] that stratification of starch-grains is the result of fermentation (dissolving effect) combined with periodic apposition is opposed by KRABBE,[3] according to whose investigations *diastase,* the starch-dissolving ferment, always acts on the exterior and never enters the starch-substance no matter how deep or variable the corrosions may appear. It must be observed that this corrosion as the result of solution by means of diastase is still an unexplained phenomenon.

The following statements will assist in explaining the minute structure of starch-grains. When a fresh starch-grain becomes dry crevices are formed in a radial direction at right angles to the stratifications. In the interior where the split begins there is a hollow space; the crevices become narrower outward. The fact that the greatest loss of water is in the interior and in the *radial* directions of the crevices indicates (1) that the entire starch-grain contains gradually more water from without inward, and (2) that in every layer or stratum the deposition of water-molecules is more active in the tangential direction than in the radial, since cohesion is less in the tangential direction.

Chemical Properties and Solution of Starch-grains.—To test the presence of starch microscopically we resort to one of the few valuable microchemical tests, namely, blue coloration with an aqueous iodine solution. Previous boiling of the starch-bearing substance in water is recommended. When the quantity of starch is very small, Arthur Meyer's plan will be found useful. It consists in decolorizing and extracting the plant-substance by means of alcohol and then adding iodine in a chloral-hydrate solution.

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[1] Stärkekörner, p. 332.

[2] Botanische Zeitung, 1881.

[3] Pringsheim's Jahrbücher, 1890.

Only the percentage composition is known which corresponds to that of cellulose: $n(C_6H_{10}O_5)$. According to Nägeli *jun.* and Arthur Meyer starch-grains do not consist of two or more starch modifications as was formerly believed by Nägeli *sen.* Red or reddish-brown coloration with iodine simply demonstrates an association with amylodextrin.

The ferment diastase, which plays such an important part in germinating cereals by virtue of its starch-dissolving effect, has already been mentioned. Its true nature and method of action is still unknown. Other substances, such as dilute acids, through long-continued action will also dissolve the entire mass of starch-grains (Nägeli *jun.*).

The behavior of starch-grains with water is especially interesting. Due to *internal* (molecular) causes, dry but otherwise intact starch-grains " imbibe " a *definite amount* of water. There is besides this *imbibition* a *swelling* due to *external* causes. This swelling is caused by a greater or lesser absorption of water at a high temperature, or by the addition of acids or alkalies. If such a swollen starch-grain is dried and again supplied with water it no longer assumes its former volume; its structure has become modified, something which never follows "inbibition" (Nägeli, Correns). Our foods (as boiled potatoes, peas, bread) contain paste (that is, swollen starch), since they have been exposed to high temperatures. This swollen starch is subsequently converted into soluble sugar by means of the saliva (ptyalin) and the pancreatic juice (amylopsin).

We shall now add a few remarks on the morphology of starch-grains, especially as to their form and size. In many instances not only genera and species but entire families may be recognized by characteristic starch-grains. Potato-starch is characterized by an excentric nucleus (hilum), and is of oval or conical form. Starch-grains of the *Leguminosæ* (seeds) are oval with a concentric hilum; those of our indigenous cereals are lentil-shaped, very small and with concentric hilum; those from the milky juice of *Euphorbia* species are dumbbell-shaped. The smallest starch-grains approach the limits of vision (1 micromillimeter = $\frac{1}{1000}$ mm. = 1μ, or less). The longest simple grains are often 185μ in length. The largest compound starch-grains measure as much as 106μ in length.

Both starch and aleuron in the cells of *Pisum sativum* (Fig. 6), are also of importance to the physiology of nutrition in man. The seeds of *Leguminosæ* contain two of the most important representatives of our food-materials: starch, a carbohydrate, and aleuron, an albuminoid; hence both non-nitrogenous and nitrogenous food-substances.

(*b*) *Aleuron-grains.*

Aleuron-grains or protein-grains ("Klebermehl" of THEO. HARTIG) form the principal *albuminoid* reserve materials in the seeds of phanerogams, while starch-grains form the chief carbohydrate reserve products. In order to observe the aleuron-grains it is advisable to fix them with a 2% alcoholic sublimate solution.[1] As a rule they are much smaller than the accompanying starch-grains; they may, however, reach a considerable size. The aleuron-grains consist of a *basal* substance and chemically different *inclusions*. The base is albuminoid; the inclusions are either crystalloids, amorphous spherical bodies ("globoids"), or calcium oxalate crystals. Of these three inclusions sometimes more than one is represented in the same grain.

(*α*) The *crystalloids* resemble the base in that they are albuminoid, but differ in being insoluble in water while the base is usually soluble. They differ from true crystals in that they store coloring material and are capable of imbibition and swelling. However, according to SCHIMPER and DUFOUR their similarity to crystals is perhaps greater than NÄGELI supposed. Schimper noticed that the regular crystalloids of *Ricinus* swelled equally in all directions when placed in dilute hydrochloric acid; while in the hexagonal crystalloids of *Musa Hillii* the swelling was equal at right angles to the main axis. In crystalloids of the Para nut the swelling parallel to the main axis was either greater or less than at right angles to that axis; hence their behavior is similar to that of hexagonal crystals in response to heat-expansion. The optical behavior is also analogous to that of crystals: the regular crystalloids are isotropic, the hexagonal slightly doubly refractive. A special peculiarity of some crystalloids is a *stratification* noticeable in the swollen state. Fig. 8 *A*, represents a cell suspended in oil; the crystalloids are not visible because they have the same refractive index as the oil.

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[1] PFEFFER studied the aleuron-grains more particularly.

(β) *Globoids* may be studied by first dissolving the aleuron and eventually also the crystalloids by means of dilute potassium-hydrate solution. The globoids are not soluble. According to Pfeffer they consist of a double phosphate of lime and magnesia. The smallest approach the limits of vision; the largest are about 10μ in diameter. They are amorphous and isotropic, and hence produce no polarizing light effects.

(γ) *Crystals of calcium oxalate* are usually found in such aleuron-grains as contain no other inclusions. They are insoluble in dilute acetic acid. They usually occur in star-shaped clusters (Krystalldrusen).

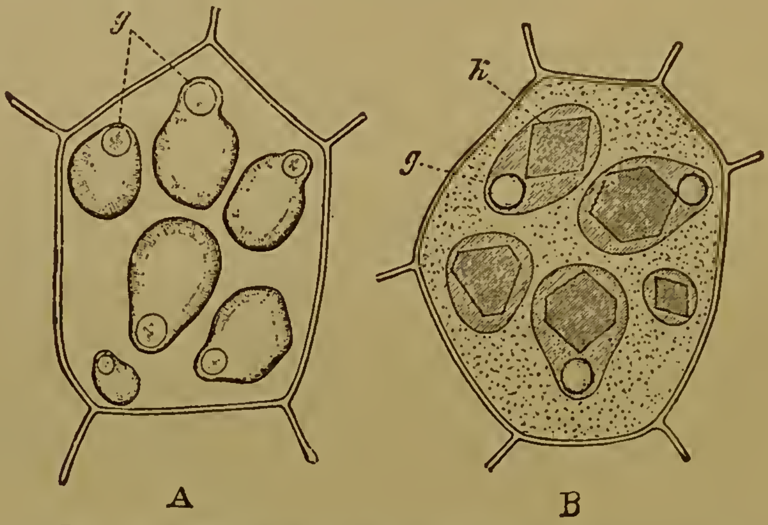

Fig. 8.—Endosperm-cells of *Ricinus communis*.

A, as seen suspended in oil; *B*, in potassium iodide-iodine solution. *g*, globoid; *k*, crystalloid. (After Frank.)

The several *inclusions* are already formed before the development of all the aleuron-grains, and are subsequently surrounded by a deposit of aleuron.

Protein crystalloids (α) not only occur in aleuron-grains, but they are sometimes also found in the nucleus, frequently within chromatophores (associated with an oily substance), and sometimes in the cytoplasm or the cell-sap.

(c) *The Remaining solid dead Inclusions of the Cell.*

Fat-crystals seldom occur, although fats are plentifully distributed in the cell. This is because the plant-fats are liquefied at ordinary temperatures and are therefore classed with the fatty oils (page 24). Solid coloring substances are found here and there (blue and violet). Some of the Schizomycetes (*Beggiatoa*) secrete sulphur within the cells. Some algæ (*Desmidiaceæ*) secrete gypsum ($CaSO_4+2H_2O$).

Calcium oxalate crystals are plentifully distributed in the cells of the entire vegetable kingdom. In most instances this lime-salt remains unchanged wherever formed. Very generally these crystals appear in the form of clusters (Drusen); frequently they occur as acicular bundles called *raphides*, less frequently as perfect crystals. STAHL studied these crystals, especially the raphides, in regard to their function, and decided that they served as a protection to the plants against destruction by snails and grasshoppers. (Feeding experiments.) Fig. 9 shows raphides; Fig. 10, perfect, well-developed crystals.

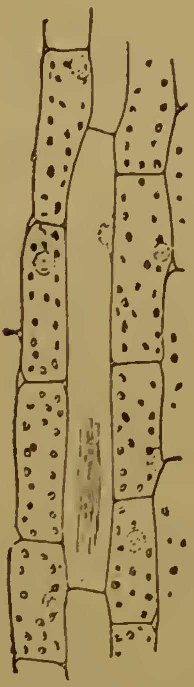

FIG. 9.—Cells from the stem of *Tradescantia zebrina*. (After Haberlandt.)

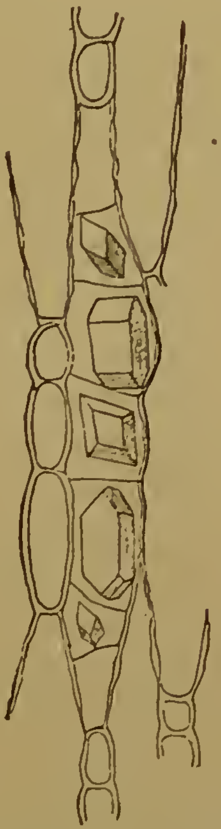

FIG. 10.—Crystal-bearing cells of *Aesculus Hippocastanum*. (After Haberlandt.)

The first more exact studies of these crystals were made by HOLZNER.[1] The perfect crystals belong either to the tetragonal or the clinorhombic system, as do also the artificially produced crystals, this depending upon whether they contain one or three molecules of water of crystallization. The clusters are aggregates of usually not very small crystal individuals around a nucleus of protein

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[1] Flora, 1864.

(albuminoid substance). Generally these crystals *originate* within the cytoplasm. As proof of such origin we have in addition to the albuminoid nucleus of the clusters the presence of an albuminoid covering to such crystals. Sometimes a wall of cellulose is formed around them. It must, however, be noted that sometimes no plasmic covering can be demonstrated.

Silicious bodies ("Kieselkörper") have also been observed within the cell.

As will be seen later, these same substances which have been mentioned as occurring in the cell may also impregnate the cell-wall. We shall here add a few remarks on *plant-mucilage*, though it does not belong to the solid plasmic inclusions. Raphide—(see cells foregoing) usually contain a mucilaginous substance. It forms the officinal *Salep* mucilage of *Orchid* tubers. It seems probable (Frank) that this substance originates within the plasm as a spherical body finally enclosing the raphides and filling the entire cell-lumen. Stahl, whose investigations concerning "plants and snails" we have already mentioned, ascribes to this mucilage enveloping the raphides the function of an "expulsor" of the acicular crystals. As soon as some animal wounds the cell, the mucilage which is under pressure partially forces out the sharp needlelike crystals. The raphides are more numerous toward the outer surface of the tubers; the mucilage is more abundant toward the interior. This mucilage also serves as reserve material, since it is dissolved when the tubers begin to sprout.—Plant-cells may also contain sphæro-crystals of calcium oxalate besides the above-mentioned perfect forms.

C. The Cell-sap and the remaining fluid Contents of the Cell.

The fluid filling the vacuoles, or more often in mature cells almost the entire cell-lumen, is called cell-sap. It contains various substances in solution: glucose, cane-sugar, inulin, asparagin, organic acids, inorganic salts, coloring materials, and occasionally still other substances. When plant-tissue is placed in alcohol, inulin is deposited in the form of sphæro-crystals (Prantl). Very often *cell-sap contains red and blue coloring material in solution.* (Notwithstanding this colored cell-sap, plasm is almost without exception colorless, leaving out of consideration the chromatophores.)

Oil-droplets (chemically not easy to define) and equally refractive *tannin-spheres*, are of frequent occurrence within the cell. Fatty oil often supplants starch during the processes of nutrition. Osmic acid reacting upon these oil-droplets is reduced to black osmium. Alkanna tincture stains the oil-globules red. Tannin-spheres and probably other chemically related substances are stained brown with potassium bichromate. According to STAHL tannic acid serves primarily as a "chemical protector" against destructive animals. (For example, snails devoured leached clover-leaves much more greedily than fresh ones.) As the author states, this fact must not be considered as all-inclusive, as tannin is very common in widely different plant-tissues. PFEFFER[1] expresses the opinion that tannin is the result of the decomposition of albuminoid substances. G. KRAUS[2] (Halle), to whom we are indebted for a more thorough study of this substance, looks upon the *antiseptic* powers of tannic acid as that property which would suffice to play an important part in the plant economy. This suggestion is highly interesting and is worthy of further investigation. Concerning my own investigations with regard to the physiological significance of tannin[3] I came to the conclusion that tannin is *erratic*; for example, in summer it wanders from above downward in the bark and vascular system of the stem of *Quercus pedunculata*; also that it stands in a genetic relation to the formation of albuminoids.

IV. THE CELL-WALL.

As soon as the plant anatomist has progressed somewhat in his work he will observe the significance of one of the points touched upon in this chapter, namely, the growth in thickness and surface of the cell-wall. The most important forms of cells are the result of localized or uniform growth in thickness of the cell-wall. Upon the growth in surface depends in general the size as well as form of every plant-cell and therefore every plant-organ. We will first treat of the internal structure and manner of growth of the cell-wall, then of its chemistry, and finally in a special chapter, of the growth-products of the cell-wall.

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[1] Physiologie, I. 306.

[2] Grundlinien zu einer Physiologie des Gerbstoffes. Leipzig 1888.

[3] Sitzungsberichte der Berliner Akademie, 1885, 1887.

A. INTERNAL STRUCTURE AND METHOD OF GROWTH OF THE CELL-WALL.

The mature cell-wall shows two internal forms of structure, stratification and striation. Both, in so far as they may be included here,[1] are usually the result of the deposition of layers containing successively *more* and *less* water, or (in stratification) they may sometimes be due to chemical differences in the substances. In stratification we are concerned with concentric layers which extend parallel to the surface of the cell-wall; in striation, with lamellae which usually extend *radially*. Viewed from the outside these striations seem to extend either diagonally or at right angles to the cell-surface. The cell-wall may consist of longitudinal, spiral, or annular lamellae, and these rings may be placed diagonally or horizontally.

The upper end of Fig. 11, *B*, shows the spiral striations of a cell cut across. The lamellae seem to be radially placed; the lower end shows the diagonal course of the striation when viewed from the inner surface. Stratification and striation mark the cell-wall into numerous delicate divisions. The various layers or complexes of layers are sometimes so combined in the same cell as to cause striation in various directions. That the difference in the amount of water present is the cause of stratification and striation is denied by some authors. These authors maintain that thickenings in the cell-wall produce striation and that "contact lines" cause stratification and striation. We will, however, follow CORRENS,[2] who has made a critical study of this subject and more recently has verified his former opinions. According to this author stratification and striation (in the true sense) are usually due to water differences, and sometimes to chemical differences in cell-wall substances (having different refractive indices). The same questions

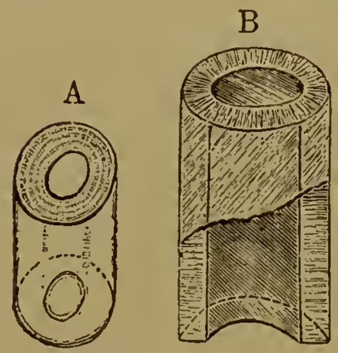

FIG. 11.
A, lamellation of cell-membrane; *B*, stratification of cell-membrane.

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[1] Delicate spiral *thickenings*, as they occur in cells of conifers, and membrane *foldings* which produce longitudinal striation in certain epidermal cells, do not belong to these internal structural changes.

[2] CORRENS, who should perhaps be considered the last pupil of NÄGELI, wrote: "Zur Kenntnis der innern Struktur der veg. Zellmembranen." Pringsheim's Jahrbücher, XXIII (1891).

which are to be considered in regard to the structure and growth of starch-grains also apply to the cell-wall. Excessive drying of the cell-wall causes the stratification to become indistinct or to disappear entirely, but it will reappear on the absorption—imbibition—of water. This proves that the stratification of cell-walls depends upon differences in the amount of water. The same is true in regard to striation. Stratification also disappears when an *excessive* amount of water is taken up by imbibition.

NÄGELI applied his theory of growth by intussusception to the stratification of starch-grains and cell-walls. The opposition to this theory still continues: scholars are divided into two distinct groups. Although Nägeli's work in regard to starch-grains is one of the greatest and most important productions in botanical science, yet the fact remains that the process of apposition, at least in regard to the growth of cell-walls, is of a wider application than Nägeli's theory would seem to permit. A refutation of the theory of intussusception is nevertheless out of the question.

According to the theory of intussusception the starch-grain within the cell increases in size at the expense of the soluble starch substance entering through the cell-wall from without, assisted by the living plasm of the cell. The cell-wall receives its building material direct from the primordial utricle. The apposition theory teaches that the strata are formed by superposition, always on the outer surface of the starch-grain, and on the inner surface of the cell-wall. There is no doubt that the lamellæ of the cell-wall are frequently formed by apposition, but the *growth of such lamellæ* is evidence that their increase in *thickness* takes place *internally*, and not on the surface. In proof of this there are certain facts concerning development to be mentioned below. Such facts, however, are also evidence of *surface* growth by intussusception. I will limit myself to the following statements.

The development of the algal group *Glœocapsa* gives additional evidence in favor of the growth in thickness and surface of cell-wall according to the theory of intussusception (NÄGELI,[1] CORRENS[2]). The outer cell-wall grows in thickness and in surface until it has increased 219 times its original volume without being in direct contact with the cell-plasm. Although this example holds true for growth in thickness as well as in surface, yet the following considerations are opposed to a surface growth by apposition. According to Krabbe[1] considerable growth in surface may be noticed in lamellæ of various bast cells which are not in direct contact with the cell-plasm. Further, there may occur *cell-wall foldings* which evidently are (Zimmermann, Kny) formed in direct opposition to the hydrostatic pressure of the cell; therefore their growth cannot be the result of expansion through hydrostatic pressure.[2] (This will again be referred to in the chapter on the physiology of growth.)

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[1] Stärkekörner.

[2] Flora, 1889. Also WILLE's contributions in defence of the theory of intussusception (Christiania, 1886).

The very frequent spiral arrangement of the molecules of cylindrical cells is also evidence in favor of the theory of internal processes of growth; this apparent twisting of the cell upon its axis is more easily explained by growth processes within the interior of the cell-wall than by processes of apposition. Phenomena of tension which become manifest when starch-grains are partially cut also point to internal differentiations.

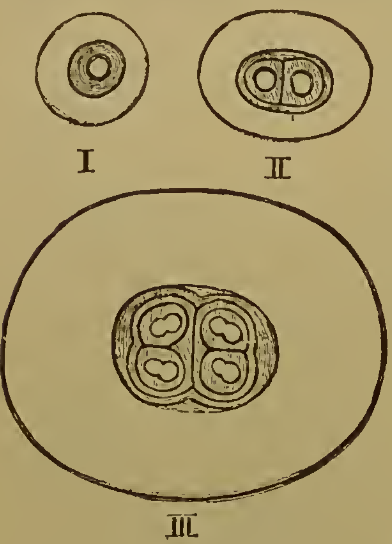

Fig. 12.

I. Single cell of *Glœocapsa rubicunda*, Kg. II. Two-celled colony of *Glœocapsa alpina*, Näg. III. Eight-celled colony of *Glœocapsa alpina*, Näg. (× 500. After Correns. II and III show the lamellation approximately correct at the periphery.)

According to the investigations of Schmitz, Strasburger, and Noll on the one hand, and Reinhardt on the other, the following statement in regard to surface-growth of the cell-wall will hold good, and will not be contradictory to what has been said before. New layers are without doubt *often* deposited by the primordial utricle while surface growth is going on; the outer and older layers are thereby passively expanded and ruptured. These layers very probably grow in surface by intercalation (intussusception). Such formation of new lamellæ must not of necessity *always* take place. According to Reinhardt's[3] investigations it is not demonstrable in hyphal fungi (*Peziza*).

The following interesting observation will aid one in judging the "theory of expansion" more critically. The advancing tips of growing cells (fungal hyphæ) were observed directly. By the aid of adhering granules it was noticed that the increase in surface was at a maximum at the place of greatest curvature, and extended only a short distance below this. The growing surface consists approximately of the hemispherical apex, with an additional cylindrical portion equal in height to the radius of the hemisphere. Under certain conditions rupturing of the hyphæ with extrusion of plasm takes place. This rupturing, however, does *not take place* at the point of greatest curvature and maximum growth in the apical area, but usually at that point below the tip where the cell-wall has acquired its greatest thickness, hence at the base of the growing part. The apposition theory, which teaches that inner lamellæ or layers are formed by apposition and outer ones are ruptured by expansion, would only permit rupture of the cell-membrane at the place of maximum growth, that is, in the region of maximum curvature, which is not the case. Rupturing takes place at the points of greatest tangential tension because of the hydrostatic pressure, not at the points of *supposed* greatest expansion. According to Reinhardt's assumption apical growth of the cell takes place in such a manner that given points lying nearest the axis at the apical area form trajectural curves outward with the advance (growth) of the apex.

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[1] Pringsheim's Jahrbücher, XVIII (1887).

[2] Supposition of the defenders of the apposition theory.

[3] Pringsheim's Jahrbücher, XXIII (1892).

The theory of intussusception is based upon deeper and more far-reaching considerations underlying the sphere of molecular physics as opposed to the more crude theory of apposition. As already indicated, the latter theory presupposes considerable mechanical expansion for the surface growth of cell-membranes. Let us follow Nägeli's[1] arguments more closely. The cylindrical cells of the alga *Spirogyra* grow considerably in length while retaining nearly the same thickness. Intussusception requires only an infinitely small reduction in the cohesion of molecules in the longitudinal direction to make it possible for new molecules to be intercalated. Tension is thus equalized, to be again disturbed by the same infinitely small difference.

No difference can be demonstrated in molecular cohesion in a longitudinal or transverse direction of the cell-wall. According to the apposition theory the difference in cohesion in the two directions must be very great, because it presupposes that layers must be torn apart in a longitudinal direction. The intussusception theory also postulates a very slight diminution in tension in a longitudinal direction.

Before dismissing this difficult subject it should be noted that

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[1] Stärkekörner, page 279 *et seq.*

Nägeli in answering the *how* of starch and cell-wall growth according to the intussusception theory expressly omits the *why* of cell-wall growth. To find the causes for this *why* is impossible according to his own statement because of the lack of knowledge in regard to molecular cohesion, tension in various directions, distribution of water and cell-wall substance, etc. In starch-grains a similar difficulty is met with, namely, the phenomenon of the smallest particles (*micellæ*) surrounding themselves with a layer of water of definite thickness. This also depends upon molecular forces "whose nature is unknown."

B. Chemical Composition and Secondary Changes in the Cell-wall.

The cell-wall is the product of living protoplasm; that is, a carbohydrate is produced from an albuminoid. The details of this chemical process are unknown.

The wall of young cells consists principally of cellulose. Its formula, similar to that of starch, is given as $n\ (C_6H_{10}O_5)$. Its molecular weight is therefore unknown. Of the microchemical reactions the following may be mentioned: swelling and final solution in concentrated sulphuric acid, in chromic acid, and ammoniacal oxide of copper; blue coloration with a solution of iodine, dilute sulphuric acid, and chlor-zinc-iodine. The cellulose of fungi is a modification of cellulose which shows these reactions only after having been treated for weeks with KHO. Before being so treated it gives a yellowish or brown reaction with iodine and sulphuric acid; it is also less affected by acids. Another modification is the "reserve cellulose," which will receive only brief mention.

Very frequently cellulose undergoes a change in composition, either throughout its entire thickness or only in certain layers or areas. The following are the most important forms of changes occurring in the cell-wall substance: (*a*) corky, (*b*) ligneous, (*c*) mucilaginous, (*d*) deposition of coloring material and inorganic compounds (mineral matter). Our knowledge concerning these is to a certain extent very imperfect.

(*a*) In a later discussion upon protection against loss of water (epidermal system) the value of *corky* cell-walls will become more apparent. The most useful property of corky or "cuticularized" (suberized) membranes is the great, though not absolute, impermeability to water. A *fatty substance* called "suberin" (Höhnel) (cutin) is *contained in the cell-walls thus changed.* Concentrated sulphuric acid does not dissolve corky cell-walls. Continued boiling with "Schulze's mixture," that is, chloride of potassium and sulphuric acid (caution!), causes the suberized membranes to form into oily drops of ceric acid. These corky membranes are widely distributed. The teleological explanation of this is that cells exposed to the air require such membranes to guard against excessive evaporation. Examples: epidermal cells, pollen-grains, spores, etc. In connection with the epidermal tissue we will refer to the waxy deposits on the outer surface of the cell-wall. (Great extensibility is not characteristic of corky cellulose membranes, as is frequently maintained.)

(*b*) *Lignification* cannot be satisfactorily explained at present. Microchemistry and analytical chemistry have explained many things, but have failed to explain definitely what lignification is or what function it serves. A well-known reaction of woody membranes is a red coloration with phloroglucin and hydrochloric acid. Anilin sulphate colors them yellow; phenol with hydrochloric acid stains them green to blue. Woody membranes resist the action of sulphuric acid more than cellulose and less than corky membranes; with iodine and sulphuric acid they turn yellow or yellowish brown. After treatment with potassium hydrate the above-mentioned cellulose reaction (blue coloration similar to that of fungus cellulose) appears. The chemical nature of woody cell-walls has been studied by various authors, among whom are Höhnel, Singer, and Nickel. The red reaction with phloroglucin and hydrochloric acid is probably due to two substances, coniferin (lignin) and vanillin. Nägeli believed the chief cause of lignification, to be a deposition of mineral salts (lime salts). The physical properties of woody cell-walls also require further study.

(*c*) There is a modification of the cell-membrane remarkable for its power of absorbing large quantities of water with considerable increase in volume; in the dry state it is hard and brittle, when filled with water it is *mucilaginous*, hence the designation mucilaginous cells. We are here concerned with various gums and plant mucilages, some of which give a cellulose reaction with iodine and sulphuric acid, while others do not. Such membranes serve to retain the moisture for the plant. Medicine utilizes the mucilaginous products of various plants. Of these may be mentioned the gelatinous stalks of

Laminaria, the gummy exudation from *Astragalus gummifer*, seeds of *Linum*, *Gummi arabicum* from the bark of *Acacia Senegal*, and other species, roots and leaves of *Althaeæ*, and the gelatin of marine algæ. The membranes of entire cell-complexes often become mucilaginous (tragacanth gum). What has been stated in regard to the mucilage of orchid-bulbs indicates that mucilage may be produced *within* the cell, hence is not always of membranous origin.[1]

(*d*) Various coloring materials are deposited in cell-walls of different plants: santalin in red sandalwood, hæmatoxylin in the blue campeche-wood, brasilin in red-wood, morin in yellow-wood, etc. In all these cases, as also in the well-known ebony (*Diospyros Ebenum*), we are concerned with a transition from phloem (Splint) into heart-wood (kernholz); or in other words a deposition of coloring substances and tannin in the originally colorless cellulose membrane. Cell-walls containing silica and carbonate of lime have been known for a long time; the former among *Equisetæ* and *Gramineæ*. Burning such silica-bearing plants after treating with sulphuric acid leaves a "skeleton." This skeleton consists not only of SiO_2, but usually also of salts of K, Ca, and Mg. The silicious membranes of the small cells in the epidermis of many grasses (dwarf-cells) serve as a protection against destruction by snails (STAHL). Incrustation of cell-walls with calcium carbonate has been observed in the hair-cells of phanerogams (*Compositæ*, *Borragineæ*); calcium oxalate occurs in cell-walls of conifers. Those peculiar excrescences of the cell-wall extending into the cell-lumen (*Ficus*, *Acanthaceæ*) containing calcium carbonate and known as "cystoliths" also belong here. According to HABERLANDT the calcium carbonate contained in the cystoliths of *Ficus Carica* (leaf) is ultimately redissolved and utilized in the metabolic processes of the plant.

C. PRODUCTS OF THE GROWTH IN THICKNESS AND SURFACE OF THE CELL-WALLS.

We must distinguish the *uniform* growth in surface and thickness of the cell-walls from the not less frequent and especially important *localized* growth. We have already touched upon that localized surface growth which causes the apical growth of a cell, and will now treat principally of growth in thickness.

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[1] FRANK'S Physiologie gives a more detailed summary.

As to development two forms can be recognized :

(*a*) At points of active cell-formation (meristem of apical areas) division proceeds so rapidly and the growth in thickness of cell-walls is so slight and so soon completed that all membranes have nearly the same immeasurable thinness. Only after cell-formation ceases or becomes less frequent, that is, at some distance from the apical area, does the characteristic thickening of cell-walls begin.

(*b*) Less commonly growth in thickness begins and *continues* immediately after the formation of the cell. In these cases the relative age of the cell-wall can be estimated by its *thickness* (examples: algal threads and cork-formation).

As has been stated, growth in thickness may be uniform and may show all gradations from minimum to maximum, that is, up to total occlusion of the cell-lumen (Fig. 13, *a*, *b*, *c*).

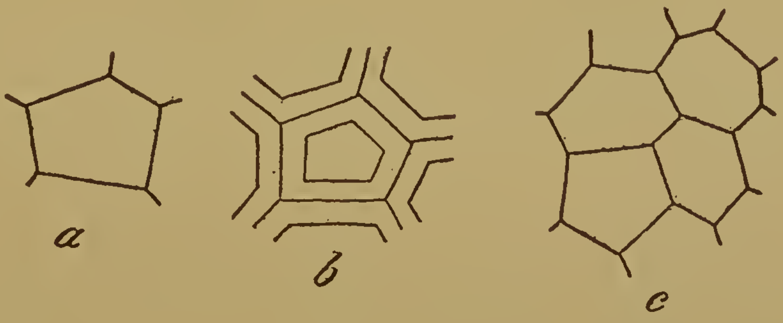

Fig. 13.

Of the very frequent unequal cell-wall thickening I will mention first the "collenchymatous." Cells showing this thickening belong to the mechanical tissues and are characterized by thick angles (Fig. 14). The selection of the name "collenchyma" (χόλλα, lime) probably depends upon the fact that certain cells with walls of unequal thickness and at the same time *gelatinous* were so named. Collenchyma is, however, not capable of swelling to any considerable extent (Ambronn).

The other forms of localized growth in thickness of cell-walls may be grouped as follows :

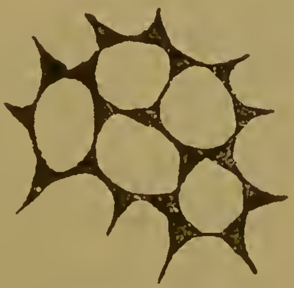

Fig. 14.

I. Spine or wart-like thickenings (usually projecting outward).

II. Linear or fibrous thickenings (usually projecting inward).

III. "Porous" thickenings; that is, thickenings with the exception of certain areas called "pores."

The following considerations will be of interest more especially from the physiological point of view :

I. This form of cell-wall thickening is usually met with in isolated cells whether they are bounded by air or water. In the atmosphere we find the spores of cryptogams, pollen-grains of phanerogams; in water the unicellular algæ. The thickenings evidently serve definite purposes, some of which are as yet not made clear. The spines of pollen-grains assist in adhering to the stigma where the formation of the pollen-tube begins; spines of spores no doubt serve the purpose of fastening them to the soil or other substratum. They also favor the transportation of pollen-grains by insects.

II. *Linear* thickenings are of the greatest importance for certain life-functions of the more highly organized plants. The remaining portion of the cell-wall of such elements is usually very thin. The thickenings serve as *mechanical support against radial pressure.* To understand their use it is necessary to be somewhat more explicit. The figures (Fig. 15) give a fair idea of the external appearance of these elements and require but little explanation. They represent portions of *vessels.* By vessel is meant a row of cells converted into a tube, having characteristic cell-wall thickenings and being essentially a *lifeless* structure. They are formed by the partial or total absorption of the transverse partitions of cell-

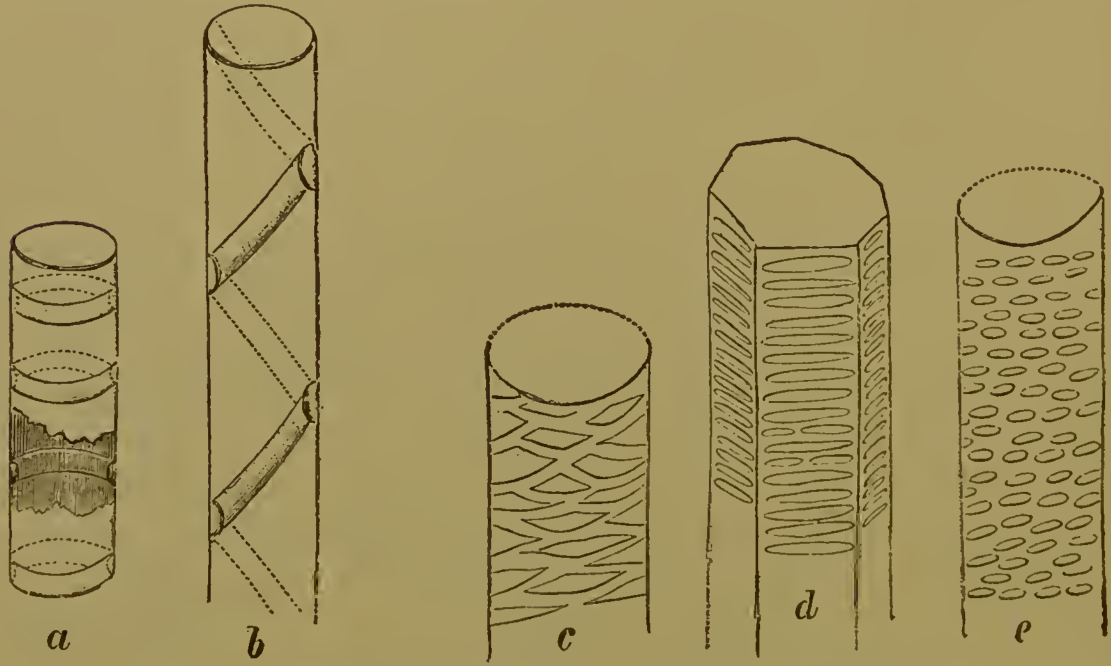

FIG. 15.—Schematic lateral view of various vascular forms.

In *a* and *b* the proximal surface is supposed to be removed, showing the distal halves of the rings with their cut ends.

rows. They are lifeless because they no longer possess a primordial utricle. It is these *vessels* that are characterized by the *thickenings* under discussion.

The designation *annular* (ring) and *spiral* vessels for *a* and *b*, and *reticulated*, *scalariform*, and *porous* (pitted), for *c*, *d*, and *e*, need no further explanation. The five forms represent mechanically supported tubes serving the purpose of conducting water in the plant-body. Why mechanically supported? Because they are contiguous with living cells, and these living cells are capable of exerting a high hydrostatic pressure, and actually force water through thin portions of the cell-walls into the vessels; otherwise they wonld be compressed by the living cells, since they are not capable of exerting any active pressure themselves. Such is the purpose of the thickenings described. Further, it is known that vessels contain alternately air and water, and that when branches are cut under mercury or colored liquids the vessels become filled to a given height with these liquids. (This is also true of mercury in spite of its capillary depression.) Therefore there is at times a negative pressure within the vessels, which again necessitates mechanical support. The structural relations are thus teleologically explained. Annular and spiral[1] vessels on the one hand, and reticulate, scalariform, and porous (pitted) vessels on the other, differ very materially in one respect. This difference may be indicated by the designation *primary* (*a* and *b*) and *secondary* (*c*, *d*, *e*). The following will serve to explain it.

In general only thin portions of cell-walls are capable of growth. From this it follows that annular elements are given considerable scope for growth in length by the localized surface-growth between the rings thus forcing them farther apart. Also the spirally thickened elements, whose spirals are at first closely wound, grow at the thinner portions, causing the spirals to become more slanting. Annular and spiral vessels stretch in a longitudinal direction. Such growth of thin-walled portions, accompanied by elongation of the entire element, cannot take place in the vessel-forms *c*, *d*, and *e* because of the firmly adhering *longitudinal* thickenings. This again explains from a teleological standpoint why a plant-organ contains or develops annular and spiral vascular elements during the period of growth, and that during the second period, that is, when growth in length has ceased, the *secondary* non-elongating vessels are more suitable. In passing it should be noted that spiral vessels often contain a number of parallel fibres (sometimes as many as twenty); also that spirals as shown at *b* (Fig. 15) are designated as *sinistrorse* in botanical terminology (beginning at the side facing the observer they extend upward from left to right).

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[1] The German expression "*Schraubengefäss*" (screw-vessel) is more correct.—TRANS.

The tracheids of insects and the vessels of plants are formed upon similar physiological principles.

So far only the surface view of the thickened walls of *secondary* vessels (*c*, *d*, *e*) has been presented, in order to avoid confusion. The view, corresponding to the outermost surface (=highest focus of the microscope), does not show us the entire structure of these organs. In III we will study the profile view of these vessels (hence cross-sections).

There are a number of special cases belonging to the category of fibrous and linear thickenings. For the most part these will be referred to in the discussion of special structures of tissues and in the chapter on reproduction. Here will be mentioned only the thickenings of the guard-cells of stomata and the membrane-thickenings of the dynamically active cells which cause the opening of anthers. Two isolated instances may yet be mentioned as belonging here: the thick pillars in palisade-cells of *Cycas* leaves, which very probably serve as a protection against longitudinal pressure during dry periods; and the cellulose projections from the inner surface of the cell-wall of the marine alga *Caulerpa*, which apparently serve to prevent the collapse of the cell, since no septæ are present.

III. "Porous thickening" sounds almost paradoxical, yet we will use this expression to designate that form of growth in thickness which affects the entire cell-wall with the exception of very small circumscribed areas. These small areas which remain thin are called pores (pits). The term pore in plant anatomy, therefore, does not mean an opening through the cell-wall, but an area which has remained thin.

Physiological considerations will explain in general the uses of such formations (see Fig. 16). The interchange of fluids from cell to cell (living cells) takes place primarily through the primordial utricle; also through the cell-wall, the dialyzing resistance of the same being less in proportion to its thinness, other things being equal. This latter is true of both living and dead cells.—I may state here that more recent investigations have demonstrated very delicate plasmic connections between cells (Tangl, Moore, Gardiner, Russow, Strasburger, and others). Upon these discoveries future investigators may base important conclusions of a widely different nature; as, for example, the transmission of irritability. This will not, however, be further mentioned at this point; we will maintain that pores facilitate the interchange of fluids from cell to cell, as well as between cell and vessel (tracheid).

These pores or thin cell-wall areas are often of circular or oval form, again linear or simply fissure-like. The accompanying figure represents various forms of ordinary pores.

a, shows fissure-like pores; *b*, right-hand side, shows rounded and oval pores, all in surface view; *b*, left side, shows the corresponding pores in profile, that is, in vertical section through the cell-wall. Here the pore is shown to be a *canal*. It may be stated that as the rule pores of neighboring cells *meet each other*; to this there are exceptions.[1] It is also the rule that these canals pass through the cell-wall at right angles. Upon the number of pores in a given cell-wall area the prevailing *direction* of the interchange of food materials may be based. Without further elucidation it is evident that thin-walled cells (for example, most assimilating cells) do not require pores, though there is extensive interchange of food-substances between them and other cells.

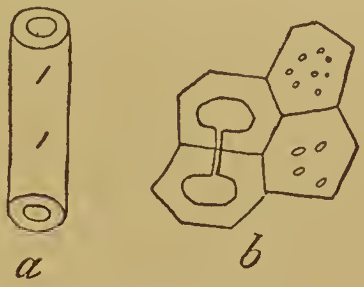

Fig. 16.

The rounded or oval pores are typical in those moderately thickened elements which function chiefly in nutrition; such as the storing and conducting parenchyma cells of pith and cortex, the storing and conducting cells of medullary rays and wood-parenchyma. These will be further discussed later. The above-named linear *fissure-like* pores are characteristic of mechanical cells. It is evident that cells which are destined to withstand pressure or tension may still perform this function though devoid of life, since the dead cell-wall constitutes the most important part. The pores in mature mechanical cells therefore appear to be harmful, since they form interruptions in the continuity of the cell-wall substance. But so long as these elements, which later subserve a purely mechanical function, grow, they must be nourished, and indeed richly. The necessary supply of cell-sap is facilitated by means of the pores. Secondarily it may occur that cell-sap is conducted through the spiral vessels and other matured mechanical cells during the entire life-period of the plant. In such cases pores are a necessity for mechanical cells. Nevertheless it is evident that porosity does not materially interfere with the proper function of such cells. In typically mechanical cells pores are therefore scarcely noticeable. As a rule they extend diagonally, more rarely longitudinally.

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[1] Such cases require further study. In advance it may be stated that their explanation will probably throw light upon new adaptations.

We shall now consider a new form of pore. Pores heretofore considered (Fig. 16) are called simple, ordinary or *unbordered* pits or pores. This new form of pore is called a *bordered* pore or pit.

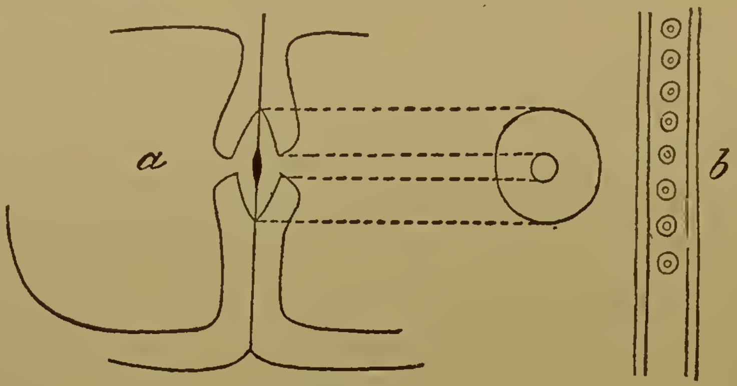

Fig. 17.

a shows a bordered pit in cross-section, which also explains the appearance in surface view as shown at *b*.

The two pore canals of bordered pits meet *funnel-like*, that is, the two large thin membranous surfaces come in contact. This membrane is therefore much larger than the diameter of the pore-canal (see Fig. 17, *a*).

Physiological anatomy still has here an opportunity to solve an interesting problem. For the present we must be satisfied with the suggestions of the greatest tissue physiologist, Schwendener, in regard to the structure of these *bordered* pits. Schwendener supposes the following arrangement. The presence of a large thin membranous area to facilitate the exchange of fluids while the cell retains the greatest possible firmness. This seems to be a very rational explanation. However, as already stated, we have no exact knowledge of the function of these structures. Another hypothesis (Russow) supposes an arrangement for ventilation which is based upon the presence of the "torus," that is, a thickened central portion of the closing membrane (see Fig. 17, *a*). This torus may be forced to one side or the other of the pore-canal entrance by excessive pressure. Schwendener succeeded in forcing water through stoppers of wood which consisted mainly of tracheids by employing considerable pressure (3–4 atmospheres), and the quantity of water pressed through was proportional to the pressure. But according to PAPPENHEIM's more recent investigations[1] and Russow's earlier observations (1877) a pressure of *one atmosphere* suffices to *force the torus against* the pore opening, and the amount of water passed through is thereby reduced (Pappenheim). GODLEWSKY supposes the torus to function similar to a platinum cone used in the chemical laboratory. According to this investigator the margin of the torus is crenated, and fine radial thickenings or something similar are supposed to extend from the margin of the torus over the margin of the closing membrane (*margo*). In this way the *margo* when pressed against the pit cavity acts similarly to a folded filter; the crenated margin of the torus prevents the tearing of the filter, and still permits the passage of water.[2]

Bordered pits are therefore all those thin cell-wall areas of the above-mentioned secondary vessels; consequently not only of porous vessels but also of reticular and scalariform vessels. Accordingly a cross-section or profile view of two contiguous cell-walls of a scalariform vessel, for example, would appear as shown in Fig. 18. A surface view of the same pits is represented at the right in the figure.

We will now pass to the *localized surface-growth* of the cell-wall. We have already become familiar with one instance of the elongation of annular and spiral vessels. Another instance is to be observed in cell-division (rather the preparation to divide) of the alga group *Desmidiaceæ*. Their asexual development takes place through division. Fig. 19 explains itself. We are here concerned with the zone which lies in the region of the constriction of the cell; it is the growing zone. After the elongation of this zone a septum is formed in its middle portion.

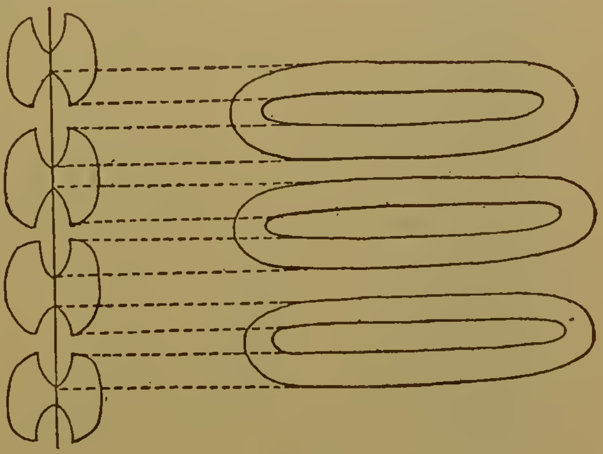

FIG. 18.

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[1] Berichte der deutschen botanischen Gesellschaft, 1889.

[2] RUSSOW's communication "Zur Kenntnis des Holzes, etc.," is to be found in Bot. Centralblatt, XIII; GODLEWSKY's communication in Pringsheim's Jahrbücher für wissenschaftliche Bot., XV (1884).

A frequently discussed example (discovered and studied by Pringsheim) is the growth in length of the alga *Oedogonium*. Here we are not concerned simply with a localized surface growth of a cylindrical membranous zone; the complication therein lies in the fact that the inner layer of the zone is undergoing active growth while the outer layer of the same zone becomes torn (Fig. 20).

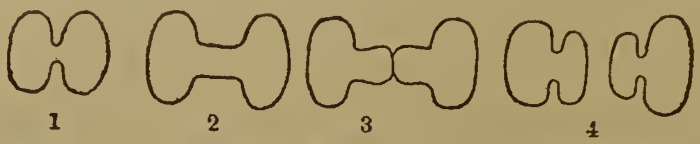

Fig. 19.—Division of a desmid-cell (diagramatic).

First the cellulose-ring is formed, projecting inward (*w*). The smaller Fig. 20, *B*, represents the time-period at which the circular tearing of the outer membrane has taken place (*w′*), and the elongation of the cell takes place at the expense of the cellulose-ring. After elongation is completed a new septum forms. Repetition of this process gives rise to the "caps" represented in the larger figure (five caps at *c* in Fig. *A*), and a corresponding number of sheaths, which are directed upward, are formed by the projecting edges of the repeatedly ruptured cell-wall. These sheaths are just separated from each other, and each one lies in the vicinity of a transverse septum.

Besides the instances already mentioned there are a series of growth phenomena belonging to this category, as is evident from the consideration of those spongy and stellate tissues in leaves and water-plants. Primarily all cells are in close contact. Three cells may enclose an intercellular space (*i*, Fig 21), which space is the result of peculiar localized surface-growth of the cell-membranes.[1]

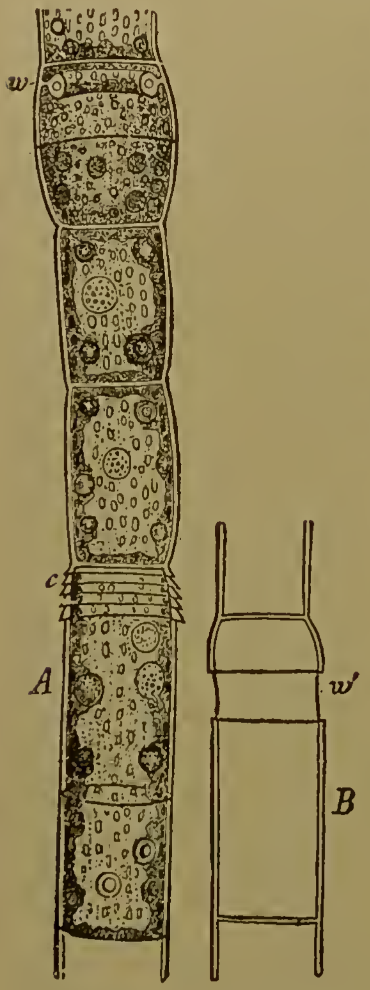

Fig. 20. (After Sachs.)

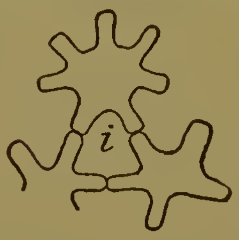

Fig. 21.

We have been obliged to mention some very important cell-forms in this section. By way of completion we will add some general remarks on *cell-forms* and their names, since the expressions and terms concerned pertain to the most valuable language-treasure of scientific botany.

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[1] Compare Zimmermann's Beiträge zur Morphologie und Physiologie der Pflanzenzelle, Heft 3, 1893.

The terms *parenchyma* and *prosenchyma* have long been established. They do not refer to the mode of growth, but simply to the form of the cells. The term *parenchyma* is used to designate: 1, all *isodiametric* and *tabular* cells (hence all spherical, cubical, parallelepipedal, and polygonal cells); 2, all elongated cells having blunt ends (hence all elongated cells with exactly or approximately rectangular ends). *All elongated cells with pointed or sharp endings* (hence conical, one or both ends blade-like) are *prosenchymatous.* The most important representatives of *prosenchyma* are the mechanical cells (skeleton-cells) which were named "sterome-cells" or "stereids" by SCHWENDENER.

With HABERLANDT we use the term *sclerenchyma*[1] to designate *considerably thickened non-prosenchymatous* elements which occur isolated or in groups in various tissues *exclusive of vascular bundles;* therefore in the outer cortex, pith (medulla), etc. Two sclerenchyma-cells in cross-section are shown in Fig. 22.

A fitting introduction to a brief consideration of the origin of new cells is the statement of a fact which sometimes causes difficulties to the beginner in phytotomy; it is that every cell has a membrane. This statement holds good for every tissue-structure. On maceration (carefully boiling, for example, a particle of wood in sulphuric acid and calcium chloride) the tissue separates into its individual elements. Even an immeasurably thin wall between two cells of a mature tissue is thereby split and shown to be double. The macerating liquid has dissolved the cementing material. This leads us to the so-called "primary membrane" or "middle lamella," which is, however, not wholly identical with the intercellular cement. The prominent, not immeasurably thin, middle lamella of woody cells differs from the remaining membrane in having a different refractive index. Solubility in the macerating mixture is therefore

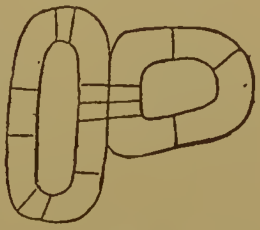

FIG. 22.

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[1] DE BARY (Comp. Anatomy) designates typical mechanical cells as "sclerenchyma fibres"; hence the terminology here introduced differs markedly from that of de Bary.

only a property of the *innermost part* of the middle lamella, which part Dippel designated as the *middle plate* or *intercellular substance.* This middle plate of the middle lamella is common to two contiguous cells; on either side of it lies the outer layer of the middle lamella, each one belonging to one of the cells. The outer layer of the middle lamella is soluble in *concentrated* H_2SO_4, while the middle lamella is not.

Finally we will mention that, similarly to the middle lamella of the outermost surface of the cell-wall, the surface turned toward the primordial utricle is also lined with a highly refractive thin membrane, the *inner membrane* of Wiesner, which according to this author is rich in albuminoid substances.

It has been discovered recently that some intercellular spaces are lined with plasmic substances. Whether the occurrence of this plasmic substance is general or not we must for the time leave undecided.

V. THE ORIGIN OF CELLS.

Science knows no other method for the origination of cells than the development of *new cells from pre-existing ones.* The first plants which existed on the earth, hence also the first plant-cells, owe their origin to a command of the Creator issued to lifeless matter: "Let the earth bring forth. . . ." The Bible and science complete each other. The latter answers by investigation the question as to the method of the origin of new cells from pre-existing ones. It can give no natural method for the origin of the first plant-cells.[1]

There are various ways in which plants may form new cells from pre-existing ones. Because these various ways are sometimes not sharply defined, it is at once evident that to obtain a clear idea of what does take place it is necessary to discuss typical cases.

We distinguish four types of cell-formation, as follows:

I. *Cell-formation by rejuvenescence*, or *direct cell-formation.*
II. *Cell-formation by conjugation.*
III. *Free cell-formation.*
IV. *Cell-formation by division* (*meristematic*).

I, II, and III are essentially concerned in the *reproductive* processes of plant-life, that is, they serve to propagate the *individ-*

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[1] This introductory paragraph, to say the least, is very unscientific. It does not assist the advance of science.—Trans.

ual; IV, on the other hand, is of the greatest importance in the vegetative life of the plant (growth, tissue-formation).

I. *Direct Cell-formation.*—The mother-cell, with its entire contents, excepting the membrane, takes part in the formation of the daughter-cell. The life of the mother-cell passes directly into that of the daughter-cell. The visible phenomenon connected with this process is the contraction, due to internal forces, of the primordial utricle of the mother-cell, and the subsequent deposition of a new cellulose membrane either while yet within the old membrane or after its escape from the same. The membrane of the mother-cell is destroyed. Example: swarm-spore formation in the alga *Stigeoclonium insigne* (studied by Nägeli).

II. *Conjugation.*—The contents of *two* externally not dissimilar cells unite to form one new cell. Either the contents of one cell pass into the lumen of the other cell by means of outgrowths from the membrane and after the opening of the contiguous membranous areas, or the contents of both cells unite by moving toward each other and fusing. The united cell-contents are then surrounded by a new membrane. Example: *Spirogyra* and similar algæ (Fig. 23).

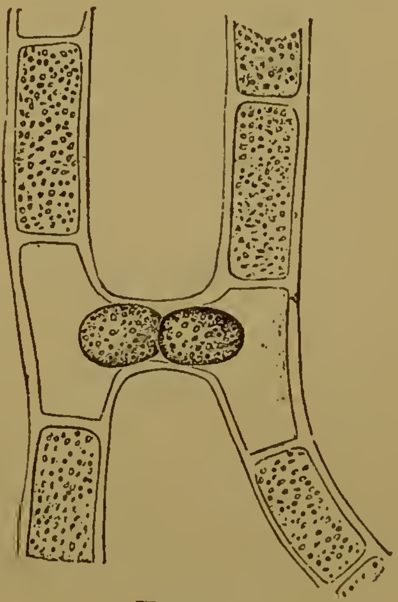
Fig. 23.
(After Berthold and Landois.)

III. *Free Cell-formation.* — The daughter-cells appear floating in the contents of the mother-cell. Small particles are differentiated within the plasmic contents of the mother-cell and surround themselves with a new membrane. This process is, however, connected with *nuclear division.* Example: ascospore-formation in asci of the fungus-group *Ascomycetes.* In this process the entire plasmic contents of the mother-cell are not utilized (Fig. 24).

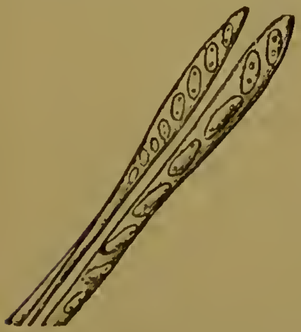
Fig. 24.—Asci with spores of *Peziza aurantia.* (After Berthold and Landois.)

IV. *Meristematic Cell-formation or Cell-formation by Division.*—Septa divide the entire contents of the mother-cell. Four sub-groups are recognizable.

(*a*) Splitting up of the plasm with *complete* membrane-formation.

(*b*) Division of the plasm with *partial* membrane-formation which occurs *simultaneously.*

(*c*) Division of the plasm with *partial* membrane-formation which occurs *subsequently*.

(*d*) Cell-formation by budding.

In (*a*) the mother-cell divides into two, more rarely many, daughter-cells. As in type III they receive a complete new membrane, but differ in that the entire contents of the mother-cell are utilized. Example: spore-formation among certain moulds (Fig. 119).

(*b*) This is the more usual form of cell-division in tissue-formation. Internal causes bring about a division of the plasm; then suddenly the cellulose-membrane makes its appearance, usually at right angles to the wall of the mother-cell. Hence the daughter-cells possess in part the membrane of the mother-cell. In sharp contradistinction to (*c*) no intermediate form with incomplete septa can be observed.

(*c*) The primordial utricle becomes constricted. (In cylindrical cells, for example, there appears a circular fold.) Finally, when this constriction has progressed to the middle point, the two portions separate. Immediately following this process the cellulose-wall begins to form from without inward, sometimes presenting the appearance of a constricting membranous fold actively encroaching upon the primordial utricle. But the cell-membrane can only grow by means of the nourishing plasm; the plasmic constriction is therefore primary. Example: the algal genus *Spirogyra*. Since such division usually occurs in darkness, it is advisable to place the algæ in the dark before examining them; or the algæ may be selected at night and placed in alcohol to be examined the following day. By proper management all intermediate stages of cell-wall formation may be found.

(*d*) Budding. The mother-cell develops a bud which becomes independent by the formation of a septum. The bud may finally become entirely separated. Example: *Sacharomyces cerevisiæ*, the fungus of beer fermentation (Fig. 25).

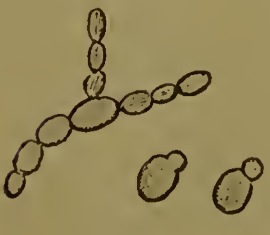
FIG. 25.

Among these plants (*Sacharomyces*) the interesting discovery has been made (REES) that they reproduce differently under different external surroundings. In the usual medium (beer) budding is the prevailing mode of reproduction. If simply kept moist, for example, upon slices of potato, the fungus reproduces by free cell-formation (ascospores). Cell-formation by budding is also typical among the *Basidiomycetes*.

PART II.

TISSUES AND SIMPLE ORGANS.

A. STRUCTURE OF TISSUES AND SIMPLE ORGANS.

The anatomist distinguishes between formed tissue, or *permanent tissue,* and tissue in the process of formation, or *formative tissue.* Formative tissue—tissue which is capable of growth and cell-division—is in general designated as *meristem.* Again, a distinction is made between short-membered parenchymatous formative tissue, or *meristem* in the narrower sense, and longitudinally extended formative tissue (more prosenchymatous in nature), or *cambium.* It is readily understood that every cambial tissue is more or less secondary in nature, for in general every organ begins with short or spherical cells (" primary meristem ").

By an *organ* is understood a cell portion, a cell, or a cell-complex, adapted for a definite function. *Tissue* is a purely morphological conception. Any coherent cell-complex having extension in at least two directions may be designated as " tissue." The consideration of the structure of organs and tissues necessarily coincides with the discussion of the structure of the plant itself, since plants are either *single cells*, *cell-threads*, *cell-surfaces*, or *cell-bodies*.

The building up or the formation of the three plant-forms last named depends on the one hand upon the *mode of cell-division*, and on the other upon the growth of the cells, *individually* and in *mass.*

A *cell-thread* or cell-filament is a cell-complex whose septa are at right angles to the longitudinal axis, or which, at least, presents no longitudinal septum when revolved upon its longitudinal axis. (Numerous examples may be found among the algæ and fungi, as well as among various trichomes of higher plants.)

A *cell-surface* is a cell-complex formed of a single layer of cells, whose septa are approximately vertical to the surface of the cell-complex, but may form any angle relative to each other. Examples: some algæ, moss-leaves.

A *cell-body* is a cell-complex in which the cells are placed side by side in three directions.

A cell-filament is formed from a single cell. This may take place (1) by the exclusive division of an *apical cell* (Fig. 26 I), or (2) by the combination of intercalary division with apical cell-division (26 II). In Fig. 26 II *a* apex and base are wanting; the cells of the filament are of nearly equal dimensions. In Fig. 26 II *b* there is a definite apical cell in which would appear the fifth septum.

A cell-surface may arise from a single cell (Fig. 27 I *a* and I *b*) or from a cell-thread (27 II *a* and II *b*). Cell-division may be wholly peripheral in that only the marginal cells divide (Fig. 27 II *b* represents an older segment of a cell-filament in which this fact is indicated), or the internal and marginal cells divide (27 II *a* and I *b*, final stage).

A cell-body may develop from a cell, a cell-filament, or a cell-surface. As soon as cell-walls in a cell appear in three different directions we have a cell-body. Here also we may consider the division of inner and outer cells independently of each other. We shall proceed at once to consider one of the most important growth-types of a cell-body.

A. *Stem-structure among Vascular Cryptogams and Mosses* (Fig. 28 *a*, *b*, *c*).—Among *Equisetaceæ* and many ferns, as well as among some leafy mosses, there is found at the *apical area of the stem* a three-sided pyramidal (tetrahedral) cell, called the "apical cell." This cell divides, forming successive spirally arranged septa. Fig. 28 *a* presents a lateral view, 28 *b* a surface view from above ("apical view"). In many instances, for example, in the "bilateral" stem of *Selaginella*, the apical cell is approximately "two-edged." An apical view is shown in Fig. 28 *c*; a lateral view is similar to Fig. 28 *a*.

Since all the cells of such an organ can be traced to the segments of the apical cell, and thus to the apical cell itself, we may with propriety speak of a *single vegetative point*.

B. *Root-structure of Vascular Cryptogams* (Fig. 29).—The tetrahedral apical cell not only forms successive spiral segments, but also *cap-segments* for the "*root-cap.*" These root-cap segments are the result of partition-walls formed parallel to the distal surface of the apical cell, as shown in Fig. 29. (In this branch of anatomy extensive researches have been made by Nägeli, Schwendener, and Leitgeb.) Other types of root-growth will be considered later.

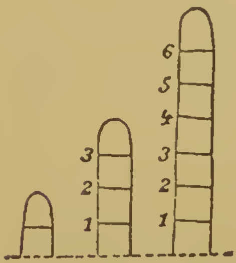

Fig. 26 I.

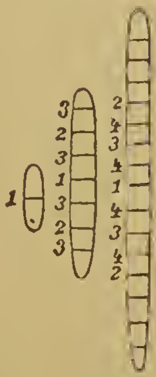
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Fig. 26 II *a*.

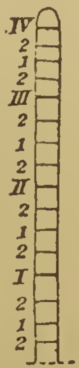
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Fig. 26 II *b*.

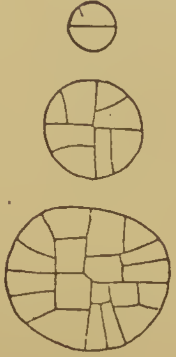

Fig. 27 I *a*.

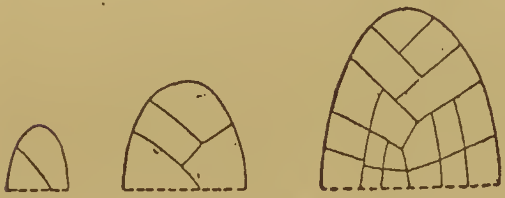

Fig. 27 I *b*.

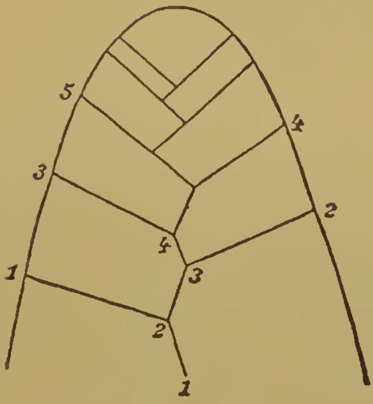

Fig. 28 *a*.

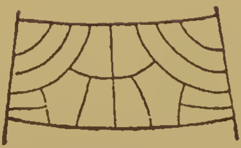

Fig. 27 II *b*.

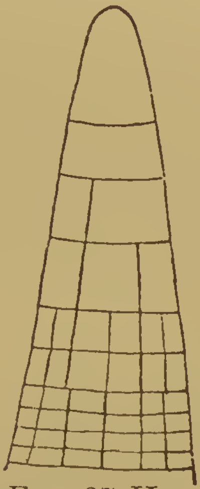

Fig. 27 II *a*.

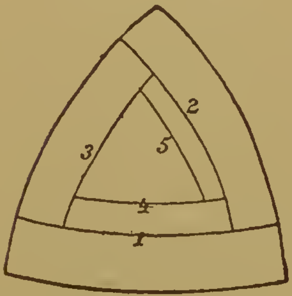

Fig. 28 *b*

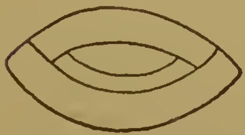

Fig. 28 *c*.

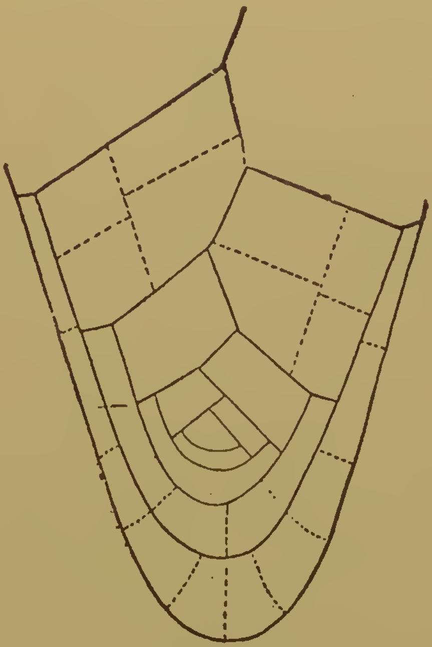

Fig. 29.

C. *The Lichen-Type.*—A collection of cell-filaments form a cell-body with an apical cone similar to the ones just mentioned. The filaments lying immediately about the axis in which growth proceeds *divide continuously.* Those lying some distance from the axis of growth seldom branch. In this form of growth any given point not lying at the apex moves forward in an "orthogonal trajectory" until the cell-body has acquired its definitive width.

The following question is important as pertaining to the subject under discussion in this chapter.

How is a tissue of similar, that is, of equally large, cells converted into a tissue of unequally large cells? Three methods will be mentioned as being especially important: (1) inequality in the length of the cell-wall formation of contiguous cells (see Fig. 30, *A*); (2) unequal growth of contiguous cells (Fig. 31); with this condition is very closely allied the so-called *gliding growth*, a phenomenon of which KRABBE has recently made a special study; (3) division in cells of equal growth may cease at different periods of time. The elongated cells in Fig. 30, *B*, are formed in this manner.

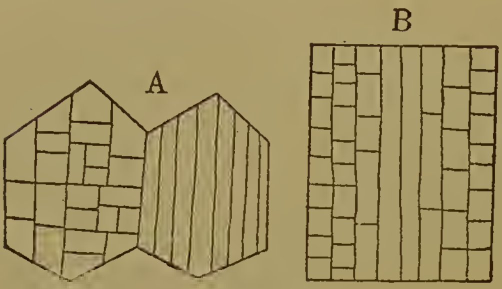

FIG. 30.

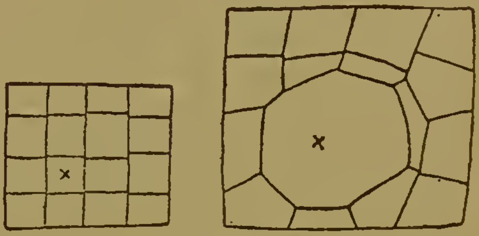

FIG. 31.

While the formation of stems and roots among mosses and in the majority of vascular cryptogams is quite accurately known and studied, and proceeds approximately in the manner indicated, the facts regarding corresponding organs in phanerogams are not so well known. Only in a few cases was it possible to demonstrate definitely, or approximately, the presence of a "single apical area." For example, four apical cells arranged in a quadrant about the axial line were observed in stems of *Coniferæ* (SCHWENDENER). Other observations (DINGLER, KORSCHELT) speak for a single apical cell. The difficulty of making the investigations explains the contradictory statements. JOHANNES HANSTEIN in his time (about 1868) sought to demonstrate the existence of a special growth-type in phanerogams. He taught that there was a special formative tissue for the epidermis, the parenchyma, and for the central tissue of the root and stem. These three formative tissues or histogens are the *dermatogen* (for the epidermis), *periblem* (for the parenchyma), and *plerome* (for the central tissue, vascular system). Though this question is still undecided, it is certain that the sharp distinction between "dermatogen," "periblem," and "plerome" cannot be demonstrated in many cases. According to SCHWENDENER the existence of the plerome as a special histogen has not been definitely proved in a single instance.[1]

B. DIFFERENTIATION OF TISSUES ACCORDING TO STRUCTURE AND FUNCTION.

(PHYSIOLOGICAL ANATOMY OF SIMPLE ORGANS.)

Differences of Functions and their Enumeration.

Although the physiological method of investigation as applied to the anatomy of plants (hence called the anatomical-physiological tendency) was not unknown in the year 1874, our knowledge concerning the relations of the anatomical structure to the life of the plant was so imperfect that anatomy in general was almost entirely separated from life-processes and became a matter of mere "dead" description. The question: Why?—in other words: Why are various tissues and cell-forms so arranged and formed?—was made applicable to the most widely different internal organs of plants after SCHWENDENER in his work "The Mechanical Principles of Stem-structure," etc., had given an important tissue-system a careful consideration from the teleological standpoint. By it the teleological method of investigation received a strong impetus. These preliminary remarks are in order, since in them lies the justification of the arrangement of the greater part of this book, especially for the extensive discussion of tissues.

We shall now consider the important tissues according to *structure* and *function*.

General considerations will show what functions predominate in plant-life and why plant-organs must exist.

The life of the plant manifests itself in three ways. These life-manifestations are: *nutrition*, *growth*, and *reproduction*. A series of special functions are dependent upon these three great life-activities.

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[1] Sitzungsberichte der Berliner Akad., 1882.

The process of plant development is, as is well known, not of unlimited duration. With the formation of *reproductive organs* or *germs* there is a relative termination of active life, which subsequently begins anew, so that we speak of a succession of *generations*. In reproduction (sexual or asexual) a plant-individual gives rise to a new individual. The mother individual, as a rule, is sooner or later entirely destroyed. Hence reproduction serves to maintain the *species*. *Growth* and *nutrition* serve the immediate maintenance of the plant-*individual*. Nutrition must of course precede the activity of growth. The inter-relation of the two is worthy of note. We shall here follow SACHS, who has very beautifully demonstrated this fact.

Growth can therefore only take place as the result of preceding *nutrition*. Ordinarily these two processes take place separately both as to time and place. When seeds germinate, when bulbs put forth leaves and flowers, when buds develop, they receive as a rule only water. Nutrition for these various growth-processes has been completed for some time, usually by the leaves of the preceding year. On the other hand horse-chestnut trees, etc., have stored within themselves large quantities of food materials as the result of the work of assimilation by the leaves during the summer months while new leaves and branches are no longer formed. Even among annual summer plants, which, superficially considered, grow and nourish themselves at the same time, a distinction in the two processes can be observed. In the night there is growth without nutrition, during day growth with nutrition. The work of nutrition is here also carried on by the mature roots and leaves, while growth takes place at various vegetative points or areas and in the flowers and fruit.

The following is an enumeration of the different special functions; most of them belong to the domain of nutrition:

I. Cell-forming function of formative tissue.

II. Structure and function of epidermal tissue-systems.

III. Function of mechanical tissues.

IV. Function of conduction of (*a*) carbohydrates and non-nitrogenous substances, (*b*) of albuminous substances, (*c*) of water.

V. Protection of embryonic areas of the plant-body.

VI. Assimilation of carbon.

VII. Function of aeration.

VIII. The taking up of food substances by means of the roots.

IX. The taking up of assimilated food-substances.

X. Storing of food-substances.
XI. Secretion and excretion.
XII. Reproduction.

As a final chapter to Functions II, III, and IV there will be added a discussion of the "endoderm," or "protective sheath."

SPECIAL FUNCTIONS.

I. THE FUNCTION OF FORMATIVE TISSUES (MERISTEM AND CAMBIUM).

The process of cell-division during the development of countless plants and plant-organs is the principal cause of growth. Growth is not equivalent to cell-division. But in the majority of the so-called higher plants the function of growth stands in close interrelation to the function of cell-division. Cell-division without growth, that is, without increase in volume, is possible. It is, however, so frequently associated with growth-processes that the considerations of the modality of cell-wall formation at the same time become considerations concerning growth-types. This is also proven by the literature relating to the earlier researches of Nägeli, as well as by the related school of evolutionary development (Kny, Leitgeb, and others).

The following statements will explain the relation of growth to cell-division.

With Sachs we distinguish three cases.

1. *Growth without Cell-division.*—This rare occurrence is met with in *Siphonaceæ*, a group of marine algæ. These plants are very large, but have only a *single* primordial utricle with various branchings or projections; they have a continuous apical growth, while the distal end is closed by coagulated plasm.

2. *Cell-division without Growth.*—This again is of rare occurrence. It is typically represented in the algal group *Sphacelariaceæ*. A single apical cell divides with a transverse septum. This cell, which is situated at the apical area of the stem, represents the growing part of the plant. As soon as the transverse septum has cut off a posterior segment this segment ceases to grow. It, however, divides into a large number of cells by the formation of numerous septa.

3. These two rather rare extreme cases are opposed by the great majority of growing organs, in which development is a combination of growth and cell-division. According to Sachs, an organ (example: stem or root) in the process of development may be divided into three regions: (*a*) the region of the apex with active cell-division and slight growth (increase in volume), (*b*) the region of intercalary elongation with enormous growth and moderate cell-division, (*c*) the region of completed growth.

According to the heading of this short chapter, the activity of the vegetative area, with and without apical cell, would belong here. Yet for reasons pertaining to the arrangement of this book this subject has already been touched upon in The Structure of Tissues.

We may designate the above-mentioned vegetative points as "embryonic areas" with terminal position; while those formative tissues whose function it is to produce growth in thickness should be designated as "internal" embryonic areas. From the activity of these vegetative areas result the mechanical and vascular tissues, and from a practical standpoint would be treated in the chapter on the tissues named. This also applies to the cork-cambium.

The *formation of secondary organs on pre-existing organs* (formation of organ-systems) will be more fully treated in a subsequent section.

If, after the mere mention of these things, the reader should ask why a chapter on the cell-forming function is at all introduced at this point, the answer may be found in the following:

A plant, whether it lives for a period of less than one year or over one thousand years, is engaged in the formation of new organs during the annual vegetative period of its *entire existence.* These developing organs must have areas which are *meristematic* in character. The most important organs (leaves, branches, roots, frequently vascular tissues, etc.) are not only formed once and endowed with a lifelong function, but are increased in number by new similar organs, and in the case of loss are uniformly replaced. Among animals certain subordinate organs, for example hairs, are endowed with a lifelong power of regeneration. However, constant neoformation of the most important organs is not the rule, while the vegetable organism is specially adapted in this respect. This "function" is inherently peculiar. Its activity is perhaps not of such great importance to the complete organism as, for example. the activity of green cells (function of assimilation); it rather brings forth or awakens the activity of vegetative areas and elementary meristematic organs which through subsequent growth and modification may subserve various functions.

II. STRUCTURE AND FUNCTION OF THE EPIDERMAL TISSUE-SYSTEM.

Living organisms, in general, are separated from their surroundings by a dermis or tegumentary tissue. The injurious influence of its local or entire absence makes itself felt in various ways. Upon examination we find that the epidermal system of plants has a threefold significance.

1. The tegumentary tissue of plants, like the skin of animals, has a *mechanical* function. The more delicate parts of plants require a more resisting covering capable of protecting them against mechanical injuries (pressure, friction, etc.).

2. The dermis of land-plants forms a necessary *protection* against *evaporation* in that it is highly impermeable to water and water-vapor.

3. In land-plants it also forms a *water-supplying system.* It forms a peripheral enveloping water-storing structure as opposed to the internal water-conducting tissue represented by the water-storing cells and tracheal system (vessels, tracheids).

These three functions correspond to suitable anatomical and other adaptations. In each of the three groups of adaptations there may be noticeable a slight development or a gradual increase up to complete anatomical conformation, according to requirements.

Epidermis may be defined as a superficial cell-covering of an organ being at least one layer in thickness. If an increase in the number of these cell-layers signifies an increase in the mechanical or water-supplying function, the phytotomist speaks of it as a "several"- or "many-layered" epidermis. Since these layers under certain conditions frequently increase with great regularity, the old expression *cork-* or *periderm*-formation has been used to designate this change more specifically. Should this change still proceed in a manner to be described later, it is designated as *bark-formation.*

Before entering into the anatomical-physiological treatment of the threefold tegumentary function it is important to note that in the epidermis and vegetable teguments in general the cells are closely united, not having intercellular spaces. This structural condition is found useful in all of the three forms of epidermal function. If the contiguous radial walls of the epidermis take a wavy course (whereby their area is also increased), it very materially increases the mechanical resistance to the separation of the contact-walls. In an actual test rupturing of the tangential outer wall took place much more readily than separation of the radial contact-walls.

The accompanying figures show two small portions of representative epidermal tissue in surface view.

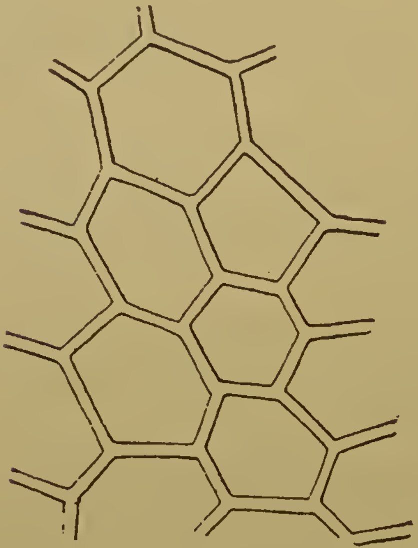

Fig. 32.

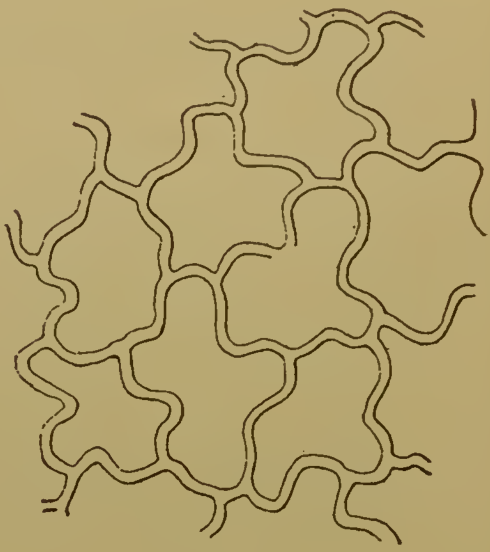

Fig. 33.

In Fig. 34 are shown all three epidermal peculiarities quite well developed. Let us consider it more in particular. The genus *Aloe* comprises plants adapted to withstand dry periods; therefore they have those anatomical features which tend to reduce the loss of moisture well developed. The *cuticle* inclusive of the *cuticular* layers (*cs* = cuticular layers, *c* = cuticle, *b* = cellulose) is very thick. The cuticula is a thin membrane highly impermeable to water. It resulted from fatty and waxy deposits in the cellulose-membrane (cuticularization). In many of our indigenous plants this cuticula is exceedingly thin, but is present in all plants; in submerged water-plants it is almost reduced to zero (No. 2).

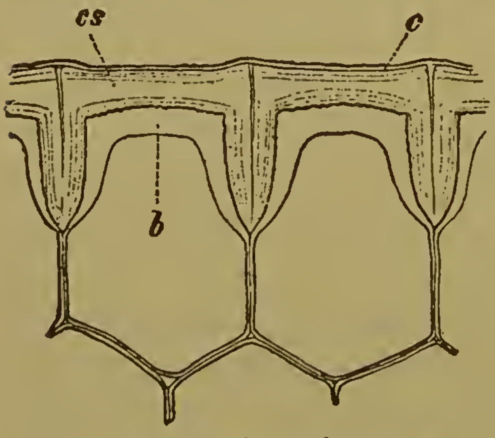

Fig. 34.—Epidermal cells of the leaf of *Aloe acinacifolia*. (After Haberlandt.)

The thickness of the entire outer wall inclusive of the thickened outer portions of the radial walls furnishes the mechanical support. In the indigenous foliage leaves which live only a few months this character is correspondingly reduced (No. 1).

As a rule, the greater portion of the epidermal cell-contents is water (No. 3, p. 53). Red and other coloring materials are frequently found in solution. *The absence of chlorophyll* is a very prominent anatomical characteristic of epidermal water-supplying tissues. We have now touched lightly upon the three functions mentioned.

In water-plants chlorophyll is very plentiful in the epidermal cell-layer. This does not at all signify that a "tegument" or "epidermis" is wanting. An epidermal water-storing tissue is, however, wanting, while we find well-marked evidence of epidermal characteristics which find expression in a considerable thickness of the outer wall, that is, mechanical characteristics, since that alone is found to be useful. For example, in case of injuries water would enter the air chambers in the interior and expel the much-needed air (see Aeration).

We speak of increase in the functional activity of epidermal systems. As a rule, the amount of water in the epidermal water-tissue increases with the depth of the single-layer epidermis and with the number of layers in the many-layered epidermis. Most of our indigenous plants have an epidermis of a single layer, with various gradations in the thickness of this *single* layer. Leaves which are exposed to considerable dryness (*Ficus*, etc.) have several layers.

As a result of excessive loss of water the *thinness of the radial walls* (Fig. 34) permits not only of shortening, but of wavy foldings. The latter, according to our conception, is for the special protection of green tissues. It can be clearly shown that epidermal and *internal* water-tissue cells are the first to suffer from loss of water. The assimilating cells may endure a much longer time without visible signs of material loss.

Certain leaves of *Bromeliaceae* show epidermal structures of several layers thickness in the part functioning mechanically as well as in the part functioning as a water-reservoir. Thin radial walls are not always present. For example, in the epidermal structures of xerophilous plants (desert plants, plants accustomed to excessive dryness) we find thick radial walls; these have, however, numerous *pores* which facilitate the exchange of water in the water-tissue.

The thin walls have, so to speak, become sacrificed to the first two functions (p. 53).

This explains the water-storing and the mechanical function of the tegumentary system. We must now discuss somewhat more in detail the function of "protection against evaporation." For a long time we have made a practical and technical use of the peculiar properties of *corky* or *cuticularized* membranes. They are used in a similar manner as by plants. Cork serves to close vessels containing liquids, to prevent leakage. Sometimes sealing-wax, resin, or some other waxlike substance is added to prevent excessive loss by evaporation. So we find *waxy excretions and waxy coatings* on plants of those climates with periods of dryness. Volkens[1] reports a desert-plant whose leaves are coated with a resinous substance. This structural change corresponds with a functional increase of the cuticula.

We now come to the consideration of *cork* and *bark*. These formations, though they may form layers several inches in thickness, are nevertheless physiologically related to the cuticle, which is frequently immeasurably thin.

Cork and Bark.—While, as above stated, the epidermis consists of a single layer of cells, the bark-covering, as a rule, consists of several or many layers of cells. Cork several layers in thickness may result from simple cuticularization of ordinary parenchyma-cells, but in the majority of cases cork is the result of a *special process of cell-division.* This process of cell-division has the greatest similarity to "cambial activity," that is, to the cell-forming process in the ring between the wood and bark (cambium-ring) of our trees.

In the case first mentioned the cork-cells do not necessarily lie in radial series, while in the latter case this arrangement is characteristic. The cork-cambium (phellogen), as well as the above-mentioned cambium between wood and bark, is, as a rule, a *bipolar formative tissue.* In only a few cases it is one-sided, that is, forms cells which become cuticularized from without inward. Ordinarily in *bipolar* cork-cambium activity the numerous outer cells become cuticularized centripetally. There are formed inwardly less numerous cells of the character of primary parenchyma called "phelloderm," or "cork-parenchyma cells." The various layers formed outwardly are not all equal: there may be alternate layers with thick and thin cell-walls (*Betula alba*).

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[1] The same investigator observed a shrub (*Reaumuria hirtella*) in the Arabian desert in which epidermal glands secrete a *hygroscopic* saline substance which absorbs moisture from the air during the night.

The well-known "peeling" or "scaling" of bark will occur very readily along the thin-walled layers, because they are only slightly extensible as compared with the thick-walled layers, in which cellulose predominates. The thin-walled layers consist essentially of suberin, a fatty substance, which, besides other constituents, contains stearin (v. Höhnel, Kügler). The microscopist recognizes cuticularized membranes by their insolubility in concentrated sulphuric acid. According to Ambronn, fat-crystals may readily be detected in the cuticle (cuticula) by means of polarized light.

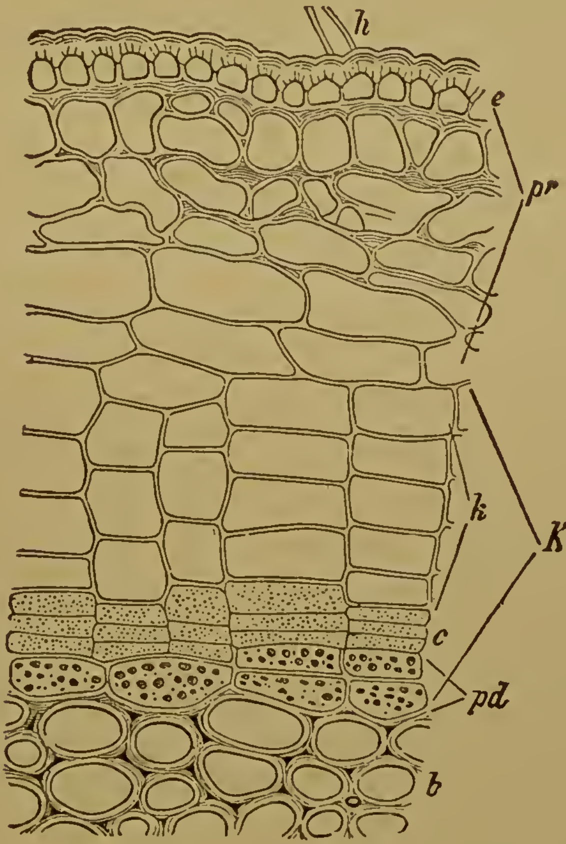

Fig. 35.—Transverse section of *Ribes nigrum* from a twig one year old.

e, Epidermis; *h*, hair-cell; *pr*, bark-parenchyma; *K*, product of the cork-cambium *c*; *k*, cork-cells; *pd*, chlorophyll-bearing cells; *b*, bast-cells. (After Sachs.)

When and where is cork-formation necessary? Harmonizing with the properties of cuticularized cells-walls, a corky protective tissue is required on the following plant-structures: at points where the cuticle and epidermis are ruptured because of the growth in thickness of the stem or root; on delicate plant-structures which are habitually or accidentally exposed; on the leaf-scars; on injured plant-tissues; on subterranean organs which must be protected against excessive moisture (for example, potato-tubers, older roots and rootlets[1]). In the chapter on Reproduction the cuticularization of the outer coverings of pollen-grains and spores will be discussed. This secondary corky change has a bearing on the ability to resist atmospheric changes for a shorter or longer time (resting period).

In all these cases a protective tissue is required. Usually this tissue has the power of continuous regeneration. We find corky tissues in older roots, in subterranean stems, on leaf-scars, and, most common of all, as a covering of the cambium-ring of growing tree-stems. Each of these cases we must discuss more in detail.

Scar-tissue (*Wundkork*).—The prick of a needle into a developing potato-tuber, or into the young stem of a woody plant, causes the death of the injured cells, and perhaps of a few others in their immediate vicinity. In nature such injuries may result from stings or bites of various animals. The *uninjured* cells surrounding the injured part at once proceed to divide parallel to the injured surface, that is, tangential to the centrally located injured cells. For example, an injury resulting from the puncture made by a needle will develop a cylindrical covering of suberized cells. This scar-tissue separates the injured (in other cases diseased) portion from the normal tissue, and at the same time prevents the evaporation of moisture from the injured surface.

Falling of Leaves.—Before the leaves begin to fall in the autumn a "scission-layer" is formed between the base of the petiole and the stem. A separation of the cells of this layer causes the leaves to fall off. In a large number of instances the formation within the scission-layer of a plate of ice which subsequently melts,[2] causes the profuse falling of leaves noticeable in the fall. The scission-layer is, however, not the protective covering. A provisional protection is formed by a mucilaginous substance known as *callus*, which closes the vessels; or by the "tyloses," that is, certain cellular protrusions which grow into the vascular system from the cells of its immediate surroundings. Drying forms a provisional protection for the parenchyma (perhaps in connection with a chemical metamorphosis which is not well understood). The final protection, however, is afforded by the formation of a layer of cork, which in some cases begins to develop some time *before* the falling of the leaf; in other cases it begins later, and permanently supplants the provisional protection.

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[1] Also on the root-tubercles of *Leguminosæ* and *Cycas revoluta*.—TRANS.

[2] MOHL, Botanische Zeitung, 1860, and Sachs, Vorlesungen.

The above-mentioned phenomena offered great difficulties to Nägeli, who in his theory of natural descent asserts that a stimulus gives rise to an organ. We ask: 1. What stimulus calls forth the formation of a scission-layer? 2. What stimulus gives rise to the beginnings of scar-tissue formation, even some time before a scar is present? To return to our subject, I will state for the benefit of those who wish to enter more deeply into these relations that the vascular system of leaves ("leaf-trace") of many growing trees is abscised three times, or even oftener, in the course of the vegetative period; first by the falling of the leaf, then again a little below the leaf-scar by the above-mentioned scar-tissue formation, and finally still deeper in the interior of the cambium by the growth in thickness of the stem (this occurs repeatedly among evergreen conifers).

The necessity for the cork-tissue formation on stems growing in thickness has already been indicated. In only a few instances can the growth of the cuticularized epidermis keep pace with the growth in thickness of the stem; as a result it is ruptured. From this follows the necessity of a new, somewhat more deeply located, layer of cork to guard against excessive evaporation. The plant behaves, if the expression may be allowed, as if it knew what would happen later. Such "knowing" is, however, excluded: the occurrence of suitable processes is only in obedience to natural laws given by the Creator. Human intelligence is capable of comprehending the *teleological* moment of these and similar adaptations. The causal-mechanics, the *causa efficiens*, of the development of cork-tissue is, however, unknown to us; this is usually the case.

Since the cambium-ring continues its activity for years, the cork-covering first formed shares the destiny of the epidermis; it is ruptured, and again a substitute is formed in the interior: that is, other cells situated more and more toward the interior become suberized.

One of the most useful exercises for the beginner in plant-anatomy is to find the exact location of the first cork-formation in stems and roots. Such investigations teach that in the stems the epidermis itself may give rise to cork-formation (*ph* in Fig. 36

B = cork-cambium). Usually it begins in a more deeply located layer of the parenchyma (Fig. 35). In roots the seat of cork-formation is, as a rule, found in the *pericambium*. Concerning this pericambium, we will at this point state only that it is a tissue one or more layers in thickness, lying within the primary root-parenchyma outside of the centrally located vascular bundle.

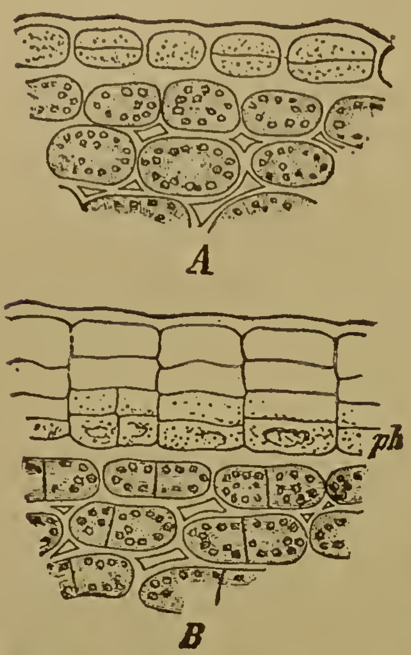

FIG. 36.—Two stages of cork-formation in the stem of *Scutellaria splendens*. (After Haberlandt.)

Cork is a complex structure, composed of different elements, but its origin can be easily determined. As a rule, it is developed according to a twofold plan—either as *ring-cork*, or as *scaly cork*. From the nature of things tissues which are separated from the sap-bearing tissue of the interior by a corky layer are subject to desiccation. It is also a rule that one and the same cork-cambium does not possess an unlimited power of growth, as is the case in the cambium-ring of our trees. The cork-cambium discontinues its cell-forming activity, while a new zone of cork-cambium appears more in the interior; this new layer bears the same relation to others, etc. Either these successive cork-layers have the form of continuous cylinders,—in which case they appear as rings in cross-section, and the bark peels off in cylindrical pieces,—or the successively formed cork-cambiums (and their products) have the form of watch-crystals or similar curved surfaces whose convexities are directed inward, appearing as partial circles in cross-section, and in some cases (*Platanus*, for example) forming scales which peel off very perfectly, leaving the stem quite smooth; in other cases the scales remain attached in large numbers for some time, the bark becomes very rough with deep crevices, and the scales are thrown off at irregular intervals. Hence "bark" at first contains the elements of the primary parenchyma between its cork-lamellæ, later also those of the secondary parenchyma, still later only those of the secondary parenchyma.

Besides the above-mentioned conditions in the case of birch-bark (*Betula*), thin-walled and thick-walled *unsuberized* cells, which are intercalated between the suberized cells, are sometimes formed in other plants. These are the so-called "scission-phelloids" of v. Höhnel,[1] which have the function of bringing about the scaling of the bark.

The scar-cork or scar-tissue has been mentioned above. When the living cells of various tissues are injured or killed, the neighboring cells are sometimes enabled to create a protective covering at once, having therefore the behavior of cork-cambium. It is not within the province of this book to enter into a discussion of practical arboriculture. I cannot, however, omit pointing out the fundamental principles underlying all those operations which are of such importance in fruit-tree culture, namely grafting. In the various kinds of grafting, such as root-grafting, side-grafting, saddle-grafting, bud-grafting, etc., injuries must of necessity occur; while in all cases an effort is made to induce the separated parts to grow together. One essential to bring about such a union is that *cambium must be in contact with cambium.* The growing together of separated tissues sometimes takes place during the natural development of plants; but caution is necessary in the explanation of such phenomena in order to avoid the mistake of pronouncing tissues as having grown together which were in reality never separated. The phanerogamic parasites form a growth-union with the host plants, while the basal parts of sympetalous (united petals) corollas have never been separate.

Structural Aids to the Function of Cork-tissue and Cuticula (cuticle).—*Trichomatic Organs* (trichomes).—In harmony with the subject under discussion the question might arise, Are there still other structures, besides the epidermal system with its cuticular and cork-formations, which serve to protect plants against excessive drying? As is to be expected, this question is answered in the affirmative. Among other works, the reader interested in this subject will find valuable information in Volkens' "Flora of the Arabian Desert" (Berlin, 1887). I will touch briefly upon the salient details.

The limitation of the entire life of desert plants to the most suitable period of the year (period of rainfall), therefore also the hastening of the vegetative period, then the transfer of the time of vegetation to the most suitable period of the year, will first be considered. The formation of roots reaching deep into the soil, the surrounding of the roots with sand and particles of earth by means of the root-hairs, which usually serve to take up food materials, the hygroscopic salts mentioned on page 56, the retention of rain and dew by means of the trichomes, must all be considered as means to the end under consideration. Along with these structural arrangements—especially the arrangement for the taking up of water—there are also adjustments for retarding the loss of moisture, such as the reduction of the evaporating surfaces; the leaf-formation may be

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[1] Wiener akad. Sitzungsber., LXXVI, 1. Abtheilung. J. E. Weiss has also written on the same subject (Denkschrift. d. K. Bot. Ges. zu Regensburg, 1890, VI).

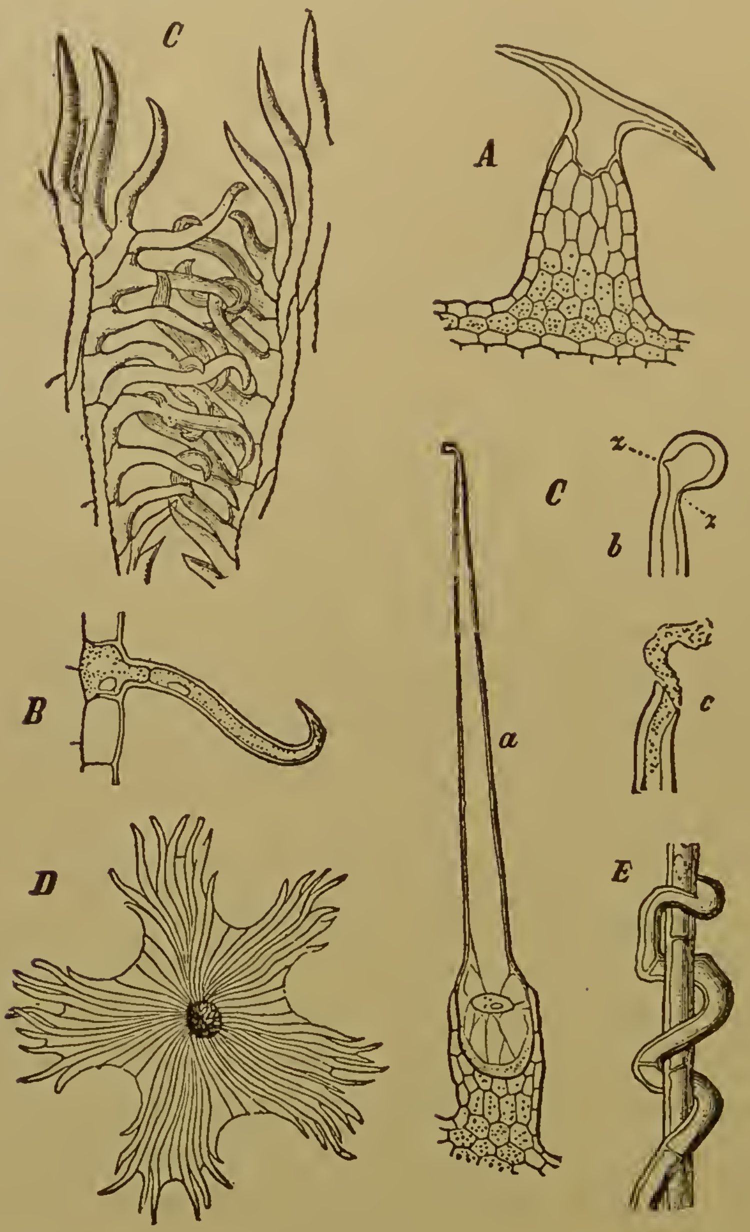

FIG. 37.

A, Climbing hair-cell of *Humulus*. *B*, Climbing hair-cell of *Phaseolus*. *C*, Adjacent margins of two pappus-scales of *Galinsoga parviflora*. *Ca*, hair-cell of *Urtica urens*; *Cb*, upper end of the same; *Cc*, the same with tip removed at *z*. *D*, Scaly compound hair-cell from the leaf of *Hippophaë rhamnoides*. *E*, Twining hair-cell of the calyptra of *Polytrichum juniperinum*. (After Haberlandt.)

absent or reduced to a minimum, in which case the stem-parenchyma alone carries on the process of assimilation; other means are the rolling up, curling, or folding of the leaf-surfaces, the vertical position of leaf-blades, and the formation of mucilaginous substances in the epidermis for the purpose of retaining moisture. Later, in the discussion of the aerating system, we will learn to know another characteristic phenomenon occurring in various forms which has to do with the position and structure of stomata (the openings of the aerating system). This phenomenon also belongs to the above-enumerated arrangements for reducing the loss of moisture.

The mention of *trichomes* made above lead me to make the following statement. The anatomy of trichomatic organs has been accurately studied; their *physiological* significance is, however, not correspondingly well known. For that reason I shall conclude this chapter rather hurriedly. Of the great variety of forms of trichomes I shall select only a few represented in Fig. 37. If a glandular hair secretes an ethereal oil, its function seems clear, namely, to attract insects which will carry the pollen. If the secretion is of a sticky consistency it evidently serves to keep off injurious crawling insects, since these take the honey without aiding in cross-fertilization. The flattened or shieldlike trichomes which cover the breathing-pores evidently serve to guard against excessive loss of moisture. The satinlike shimmer of floral leaves is due to papillose trichomes (conical projecting epidermal cells). In some instances it has been proven that trichomes with thin-walled areas near the base serve to admit moisture (rain, dew). Still a considerable number of trichome-structures remain whose physiological significance is not satisfactorily explained.

III. FUNCTION OF MECHANICAL TISSUES.

Even a superficial consideration of the plant kingdom suffices to teach that the *mechanical* influences surrounding land-plants, water-plants, aerial organs, subterranean organs, etc., are different, and that these various plants and plant-organs require definite adaptations as to the firmness of the tissues concerned in order that they (as the normal course of things teaches) may be maintained in their entirety.

In upright stems—in fact, in all organs which must maintain themselves in an upright or in a *free* horizontal position—*bending* enters into consideration, especially as the result of air currents; also of the weight of the leaves and stems, of the snow, ice, etc. The roots of a tree through whose crown the wind blows, and the grass-stem the panicle of which offers resistance to air currents, are subject to a *pulling* tension. The margins of flat leaves waving in the wind are subject to tearing and breaking. Parts of winding stems wound about dead supports, and more especially those wound about living supports (tree-stems growing in thickness), and tendrils must resist pulling tensions; likewise water-plants in rapidly flowing water, and stems of hanging fruit. Rarely there comes into play a supporting tension similar to that of a pillar, as in the case of supporting roots.[1]

The question now is, How are such mechanical requirements to be interpreted? One difficulty will be to explain these interesting relations briefly, yet not at the expense of clearness. In many respects the brief suggestions given in these lines, in other cases a hasty outlining, will assist in finding the necessary explanations.

While I shall attempt to demonstrate the mechanical principles in the internal structure of plants by giving a few examples, I shall base my discussion of the subject upon SCHWENDENER'S "Mechanical Principles, etc.," as well as upon NÄGELI and SCHWENDENER'S "Microscope."

As has been demonstrated (SCHWENDENER), there is *in the vegetable kingdom a specific mechanical tissue-system, consisting of specific mechanical cells, which in its best quality has the same supporting power as malleable iron wire, namely, twenty kilos per square millimeter (within the limit of elasticity).* These mechanical cells are designated by different authors as: stereids, skeleton-cells, *mechanical cells*, thick-walled bast, hard bast, prosenchyma-fibres, bast-cells, sclerenchyma-fibres.[2] In organs subject to bending the mechanical cells are peripherally located, while in organs subject to a pulling tension they are centrally located; that is, *in typical cases they are arranged according to rational mechanical principles.* That such an arrangement of mechanical cells is a rational one is made clear by the following elementary considerations (compare the accompanying figures, 38–42, as well as those pertaining to the root anatomy).

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[1] Aerial roots of *Zea Mays* afford a typical example. It does not seem clear why *all* vertical tissues are not subject to such a tension.—TRANS.

[2] No doubt we must wait some time before a uniform terminology will be adopted.

I. The fibres and tissue-layers of a beam supported at both ends having a weight in the middle are so influenced that the uppermost fibres are most strongly pressed together and the lowermost fibres are pulled. In the middle of the beam in cross-section there is an imaginary "neutral" fibre in which the pressing tension passes into a pulling tension. In this region pushing and pulling are at a minimum. From this it follows that in order to have an appropriate distribution of material in such a beam it must, in general, have the form (in cross-section) of two capital T's, one of which is inverted, thus (⌶), since the mass of material must be distributed at the points of greatest tension. In following out this idea one can readily understand that a *hollow cylinder* would represent a type of structure adapted to resist a bending tension from *all sides.* The combination of many double-T supports will give us a polygon whose sides are represented by the cross-lines of the T's. These cross-lines, as already stated, indicate the strongest parts of the support ("girth"); the radial connecting lines ("filling") may be much weaker; when the "girth" becomes continuous, the "filling" may be entirely omitted.

II. In the determination of the equilibrium of a prismatic staff bent to one side by some lateral force we must first of all find the "modulus of elasticity." This may be found as follows (it must be remembered that in the rational construction of this formula no fibre is to be stretched or elongated beyond the limit of elasticity): If we let A represent the area, in cross-section, of the tissue to be tested, W the maximum weight which can be supported without permanent elongation, then the supporting power within the limit of elasticity per unit of surface $U = \frac{W}{A}$. By dividing U by the specific elongation due to W, that is, $\frac{\lambda}{l}$, in which λ equals the elongation due to the tension and l the original length, the modulus of elasticity is found $E = U . \frac{l}{\lambda}$.[1]

III. Besides the modulus of elasticity, there is still another factor which enters into the determination of the equilibrium of a bent twig or staff.

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[1] In normal well-developed bast 1000 units (in length) of l equal about 13 units of λ, $U = 20$, hence $E = 1540$.

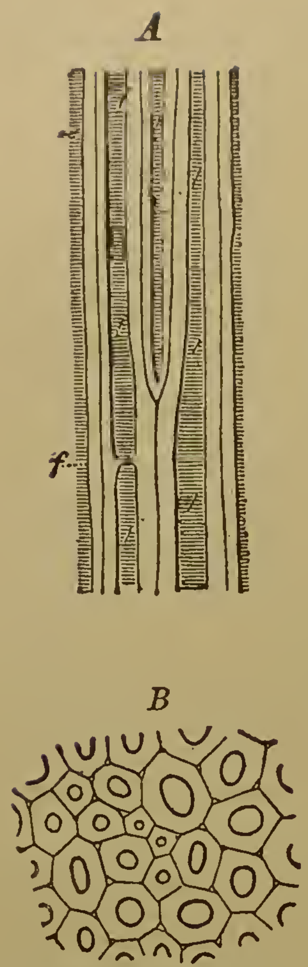

FIG. 38.—Mechanical cells in cross (*B*) and longitudinal section (*A*). (After Haberlandt.)

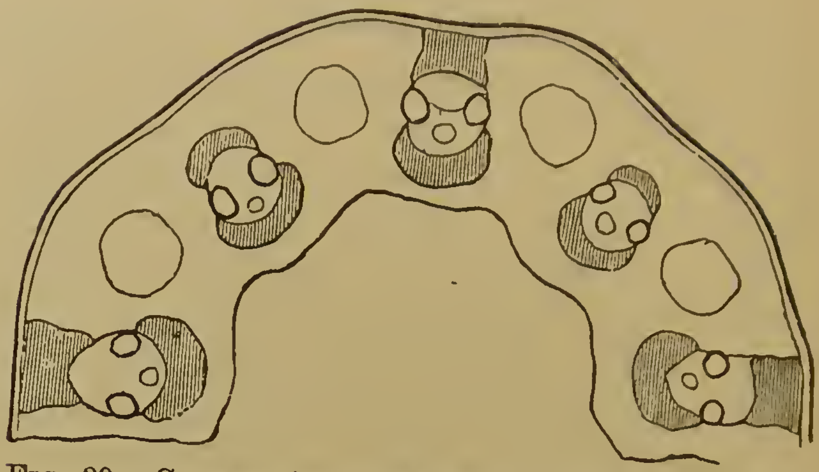

FIG. 39.—Cross-section of the stem of *Scirpus cæspitosus*. (After Haberlandt.)

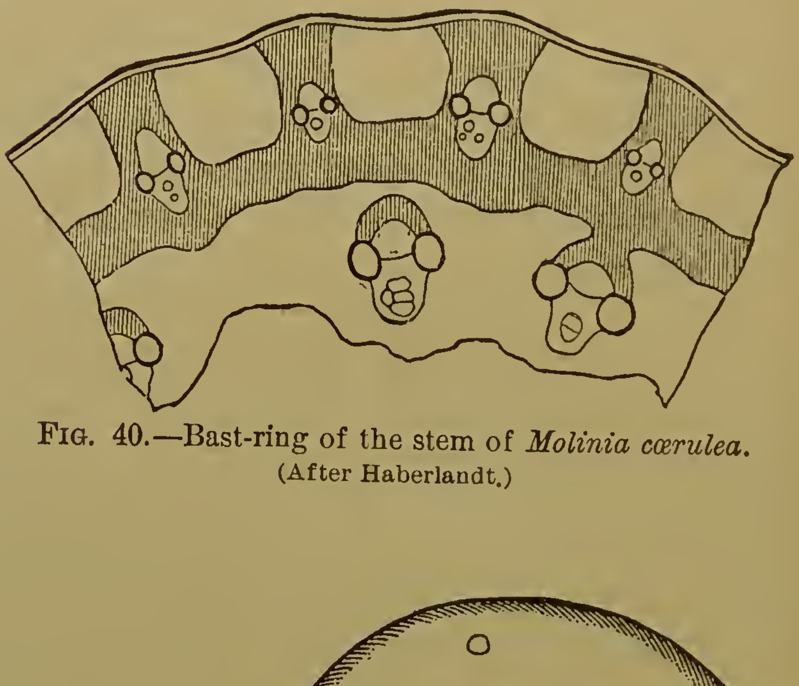

FIG. 40.—Bast-ring of the stem of *Molinia cœrulea*. (After Haberlandt.)

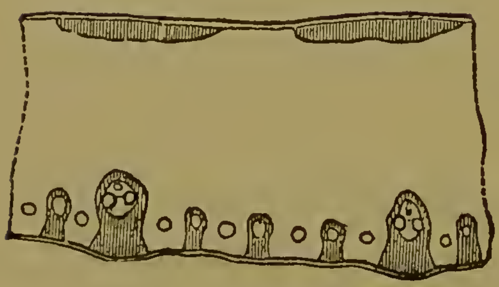

FIG. 41.—Mid-rib of the leaf of *Zea Mays*. (After Haberlandt.)

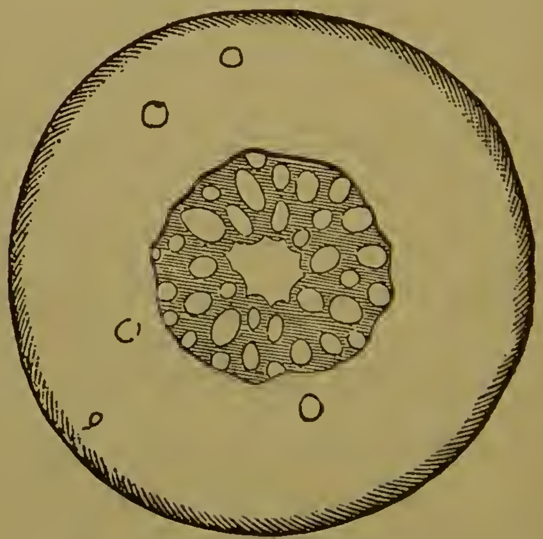

FIG. 42.—Transverse section of the rhizome of *Carex glauca*. (After Haberlandt.)

Let us make a simple experiment with a ruler. With one of its flat sides turned upward it may readily be broken by a force acting downward or upward. If the same force acting in the same direction acts upon the ruler with one of its edges turned upward, then it will scarcely be perceptibly bent. In the latter case forces inherent in the woody fibres are brought into play to counteract or equilibrate the bending force; in the former case this does not occur. From this it is evident that in order to determine the point of equilibrium there is besides *E* another magnitude, the so-called moment of flexibility (*Biegungsmoment*). The latter (*W*) is dependent upon the *form and area* of the transverse section. In the case of the ruler it is evidently the form of the cross-section, which differs in the two positions. *W* is found by multiplying the area of each element in cross-section by the square of its distance from the neutral point, and then adding the number of such products in the entire cross-section.[1] (The *limit* or *amount of flexibility* to be determined experimentally depends essentially upon *W* and *E*.)

From the above illustration with the ruler it follows that the pressing and pulling forces (of opposite elements) resulting from a lateral pressure upon a beam is *inversely* proportional to the distance of the girdings. The supporting power of the beam increases not only with the strength of the girdings, but also with their relative distance of separation; that is, the stronger the girdings the farther they may be apart in order to give a maximum effect.

This *principle of the peripheral arrangement* of firm elements in supporting organs, though simple, is most extensively embodied *in multitudinous forms* in the arrangement of mechanical plant-cells. As it is customary in technics when using two different materials—for example, wood and iron—to place the stronger material where the greatest support is to be maintained, that is, at the girding, while the weaker material is used as filling, so it is found that mechanical cells in the supporting tissues of plant-organs are peripherally arranged, while other tissues which serve the purpose of nutrition, storing of food material, conduction of fluids, etc., represent the filling material. It is to be expected that the assimilating system, dependent upon sunlight for its activity (chlorophyll-bearing tissues), and which is also peripherally located, must make suitable concessions to the mechanical tissues as to position. This is what actually takes place.

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[1] Let A equal the area in cross-section of one element, r its distance from the neutral point; then $A . r^2$ = the moment of flexibility of a given element.—TRANS.

IV. Theoretically the *strength* of a given support would depend only upon the magnitude of its cross-section. It is, however, evident that six silk threads which are about one cm. apart and so placed that one is central and the other five peripheral, are in danger of being torn by some pulling force, because tension on them is very apt to be *unequal*. This unequal tension may be counteracted to a considerable degree by bringing the threads in contact so that tension will act on all of them at the same time. The consideration of various *roots* which are also subject to pulling tensions teaches that a *central* arrangement of mechanically resisting elements is the intended plan of structure. According to a similar principle, the centripetal tendency of mechanical elements is also found in such structures as tendrils, plant-organs in rapidly flowing water, stems of climbing plants, and stalks of fruits. In rhizomes, which morphology shows to be stems, and in running stems (creepers), the anatomist finds a tendency on the part of peripheral mechanical elements to assume a more central position, hence from a morphological point of view they have a resemblance to roots. The large number of phenomena belonging to the domain of plant mechanics, which SCHWENDENER has so faithfully studied, cannot be fully discussed here. Two things, however, remain to be mentioned. Certain rhizomes living in very moist soil have the outer parenchyma supplied with air-spaces, since they are mostly surrounded by water; collapsing of this tissue is prevented by a thin peripheral layer of bast-cells. The supporting roots mentioned above (*Zea Mays*) show almost an equal distribution of mechanical elements, so that these roots are midway between typical supporting organs and flexible organs.

In such flexible *expanded* organs as the leaves the mechanical cell-complexes are in two layers, one for each surface; this is in accordance with the mechanical principles explained above (compare Fig. 41).

It must not be forgotten that thin-walled turgescent tissues represent a more or less firm substance, and in suitable positions (for example, at opposite sides of a vascular cylinder, or as filling material around the vascular bundles) it very materially assists in increasing the flexibility or firmness of plant-organs.

I have attempted to explain in a few sentences with the aid of the figures the mechanical principles involved in the anatomical structure of plants, yet careful consideration will show that the magnitude of the entire mechanical arrangement of plants may be measured thereby. Countless millions of plant-organs are subordinated to the above-mentioned principles. It must also be remembered that in the discussion of the vascular system we must again and again recur to this subject. Some related phenomena are yet to receive special consideration.

Decrease in the Firmness of Flexible Organs in an Acropetal Direction.—It would be erroneous to conclude that monocotyledons, in distinction to dicotyledons and conifers, were equally thick above and below, since they, as a rule, have no secondary growth in thickness by means of a cambium ring. The study of a grass-stem will show this. In the majority of monocotyledons the rejuvenescence upward of the monocotyledonous stem is to be ascribed to different causes from those producing rejuvenescence in the stem of dicotyledons. If the expression "becoming thinner above" were changed to "becoming thicker below," we would find that it would be more applicable to dicotyledons than to monocotyledons. It suggests that among *monocotyledons* the apical area (vegetative point) has already become somewhat "firm" before any considerable growth in length takes place. The development of the stem of a palm is quite different from the development of the stem of a dicotyledonous tree, although rejuvenescence proceeds upward.[1] This rejuvenescence, and especially the weakening of the mechanical system toward the apex, is of great importance. That this is desirable can readily be explained from a mechanical standpoint. A horizontal beam of equal thickness throughout and fastened at one end *will break at the point of attachment* if too great a weight is brought to bear upon the free end. The point of attachment is first to give way, since there the power arm is longest. If a girder is to have no weakest point, there must be a gradual increase in firmness (to be determined mathematically) toward the fulcrum or point of attachment. In its perfect form we speak of a "girder of equal resistance." RODENSTEIN[2] at SCHWENDENER's suggestions carried on some researches in which he demonstrated the presence of such perfect mechanical structures among plants.

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[1] Eichler, Growth in Thickness of the Stems of Palms, Sitzungsber. der Berliner Akademie, 1886.

[2] Structure and Life of Plants, III Vereinschrift der "Görres-Gesellschaft" für 1879.

Localized Function of Mechanical Cells.—Phytotomy reveals numerous instances of the appearance of mechanical cells and cell-complexes which have nothing to do with the flexibility and tractive resistance of organs. The *general* physiology of tissues in conjunction with mechanics will give the desired explanation of their existence. They evidently serve as a protection to the elements which conduct food substances. The layers of mechanical cells which are frequently found closely associated with the delicate tissues which conduct albumen and other substances ("leptome-bundles") are essentially protective in function. Let this explanation suffice for the present. We will again refer to this subject in the discussion of the protective sheath (endoderm, inner dermis).

IV. THE FUNCTION OF THE CONDUCTING SYSTEM.

A careful study of the few figures illustrating the mechanical tissue-system will show that the description of the anatomical structure of the stem, root, and leaves would be imperfect if only reference were made to the mechanical tissues involved. We must also discuss the *conducting* tissue-system.

We shall at the same time treat of the anatomy of the vascular system and of the mechanical system, showing the respective arrangements of the two in the great plant-groups. We shall study the more important organs in which they occur.

Consideration of the Conducting System in Itself and in its Relation to the Mechanical System.

(*a*) *The Various Cell-forms.*

NÄGELI,[1] in his researches in plant anatomy, introduced names for plant-tissues which, according to our present knowledge of the subject, have become in part useless. The writer intends to give a lucid presentation of the subject according to the present status of scientific botany, and not an elementary presentation. For that reason we must enter somewhat into a discussion of the progress of botanical science as well as of the modern change of opinions. This is important because every modern author of a work on general plant anatomy must harmonize his position with NÄGELI's conceptions of "xylem" and "phloëm."

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[1] Beiträge zur wissenschaftlichen Botanik, 1858.

SCHWENDENER's investigations of the mechanical tissue-system, and the attempt made to introduce gradually an anatomical-physiological terminology lessened the importance of Nägeli's terms, perhaps denied them the right of existence. In spite of this Nägeli's terms are still in use, and variously applied by different authors.

NÄGELI proceeded from the *cambium-ring* of dicotyledonous plants, which grows outwardly and inwardly, therefore showing a *bipolar* cell-activity. From a purely topographical standpoint he called the outwardly formed product *phloëm* and the inwardly formed product *xylem.* By applying these conceptions to plant-groups without a cambium-ring confusion arose. It could not be otherwise. At present we are certainly too far advanced in our knowledge of tissues to wish to divide them topographically. Earlier anatomists subsequent to NÄGELI observed the occurrence of mechanical cells outside of, as well as within, the cambium-ring; these authors did not all agree with Nägeli to designate similar elements by different names. Further, we very frequently find anatomical elements resembling very closely those occurring in the phloëm and xylem, namely, the thick-walled prosenchyma-fibres of *monocotyledons*, which occur as rings, ribs, etc., and are independent of any cambium-ring. One investigator may name them "hard bast," another "woody cells," both would be equally correct from an anatomical standpoint. LINK and KIESER (earlier anatomists) pronounced the mechanical ring of *Liliaceæ* and other monocotyledons to be "bast"; MOHL questioned the propriety of doing so. DIPPEL named the bast occurring in the vascular bundle "wood," that occurring outside of the bundle bast, though the cell-forms are exactly alike. SCHACHT and UNGER do likewise, but the former questions whether the term wood is here rightly applied.[1]

The author of this book is in a position to make clear the absurdity of the earlier conceptions of Nägeli. I may also refer to DE

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[1] Compare Schwendener's Mechanische Princip.

Bary's (1877)[1] attempt to introduce a scientific terminology, which Haberlandt (1879)[2] strictly adhered to and embodied in his writings. At the present time there is no author in Germany prepared to offer a *generally* acceptable terminology of tissues which could be introduced in a manual of botany. The best means of making one's self understood and of offering something useful to the beginner in scientific botany is, according to my opinion, the following: One must revert to the expressions which had their origin, in part, with the older anatomy, and which designated definite *cell-forms*, such as "vessels," "tracheids," "wood-parenchyma," "medullary rays," "thick-walled bast," "libriform-tissue," and "sieve-tubes" as "cambiform" and "conducting cells"; and further, it must be established that there are (1) water-conducting elements, namely vessels and tracheides; (2) mechanical elements: bast-cells and bastlike cells; the latter when occurring within the cambium-ring were already named "libriform" by earlier anatomists; (3) elements which conduct carbohydrates (or physiologically similar substances): wood-parenchyma with medullary rays; (4) albumen-conducting elements: sieve-tubes with cambiform and conducting cells.

These *cell-forms* (1–4) designated by definite names must be clearly distinguished. We shall now briefly consider their anatomical characteristics, which are already partly known from what has gone before.

In the mature state the vessels and tracheids are *dead* elements, since they are without a primordial utricle. Vessels are generally tubes resulting from cell-rows whose transverse walls have either entirely or partially disappeared (reabsorbed), leaving ridges, or rings, and whose longitudinal walls are strengthened by various thickenings (compare cell-structure). *Tracheids* are closed prosenchymatous dead *cells* whose *walls resemble those of the vessels.* There are "spiral," "reticular," "scalariform," and "porous" tracheids. Porous tracheids are particularly numerous; they usually have the form of typical prosenchyma-cells, and may be named *fibrous tracheids* as distinguished from the large-celled *vessel-like tracheids.* We have already learned to know the typical mechanical cells (Fig. 38) as thick-walled prosenchyma-fibres with delicate linear pores which usually extend diagonally. While the large-celled tracheids closely resemble the vessels in structure, the fibrous or long-celled tracheids represent a *form intermediate between mechanical cells and tracheal elements.* The fibrous tracheids are therefore dead prosenchyma-cells with numerous bordered pores. *They occur very abundantly* in the wood of conifers; they are also frequently intermingled with the various tissue-elements of angiospermous trees. The term "bordered-porous-libriform" is sometimes used to designate these tracheids; this term is intended to imply that they resemble mechanical cells in structure and function, but that they differ from specific mechanical cells (bast-cells and libriform-cells of trees) in having no bordered pores, but only such without borders. The absence of the primordial utricle in the mature libriform is not a characteristic of this cell-form, although it is frequently spoken of as a dead tissue, and this with some degree of justification. *Woody parenchyma* and *medullary rays* are physiologically equal in so far as both consist of living cells which at definite periods carry considerable carbohydrate as well as physiologically related substances; anatomically they also resemble those parenchymatous cells having numerous rounded simple pores; they differ, however, in their position and arrangement. Woody parenchyma usually extends *longitudinally* in the form of bundles or bands; sometimes it slants in a tangential or radial direction. Medullary rays represent *radial* bands or plates having the form of cell-surfaces or expanded cell-complexes. The individual cell of the wood-parenchyma is regularly elongated in direction of the axis of growth; the cell of the medullary ray is elongated in a radial direction, at least very frequently. The function of conduction is not only assisted by this special arrangement of the wood-parenchyma and medullary ray, but also by the numerous pores occurring in the most suitable parts of the cell-walls. In the medullary rays the pores are therefore most numerous in the tangential walls. (Cell-forms intermediate between wood-parenchyma and libriform are named "substitute fibres" (*Ersatzfasern*) by Sanio.) A more or less theoretical observation may be introduced here, namely, that cells resembling wood-parenchyma also occur outside of the cambium between the cortical medullary rays. This might be a reason why the term "woody parenchyma" should be rejected, since this cell-form occurs not only in the woody parenchyma, but also in the inner cortical tissue, as well as within and also outside of the monocotyledonous vascular bundles. But because of the fact that the term has become firmly rooted and that it is used with some degree of justification such a procedure is not advisable. It should, however, be observed that wood-parenchyma and medullary rays together form an anatomical-physiological system. From this standpoint, therefore, the ray-parenchyma cells and the wood-parenchyma cells, whether they occur within or outside of the cambium, may be named alike, as is likewise done in the case of the mechanical cells. According to the proposition advanced by TROSCHEL (1879), a pupil of SCHWENDENER, the entire conducting-parenchyma (medullary-ray tissue and longitudinal bundle-parenchyma) contained in the conducting bundles might be designated as "amylome." To me the term *fascicular conducting-parenchyma* seems to be preferable, since it at the same time points out the important fact that there is also an *extra-fascicular conducting-parenchyma*, namely, the parenchyma of the vascular bundle-sheaths (in leaves, petioles, etc.), and the cortical parenchyma of stems and petioles. As already stated, these structures are concerned with the circulation of carbohydrates and physiologically related substances, such as inulin, etc.

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[1] Comparative Anatomy, p. 330, *et seq.*

[2] Entwickelungsgeschichte des mechanischen Gewebesystems.

Finally, we will briefly mention the *sieve-tubes* with the *cambiform* and *conducting-cells.* The fundamental characteristic of this tissue is softness, whether the cell-walls are thin or comparatively thick. The ultimate anatomical-physiological difference between cambiform and conducting cells must now be more clearly defined.[1] These tissues afford a difficult study when considered from the point of mere anatomical description. *Sieve-tubes* are usually elongated cells with rather thick, sometimes thin, longitudinal walls and horizontal or diagonal transverse walls; *the latter*, sometimes also the longitudinal walls, *contain minute perforations.* These thin, perforated cell-wall areas are designated *sieve-plates* or sieve-disks. In much-inclined transverse walls there are usually several sieve-plates; in the walls that are horizontal or only slightly inclined there is usually only one. The sieve-plates are *perforated* and not porous. These openings permit the circulation of undissolved mucous albuminous substances.

The accompanying figure (43) shows the structure of a transverse wall which has been converted into sieve-plates. This figure represents their appearance during the summer. A noteworthy change takes place in these sieve-plates during the winter: the entire sieve-plate septum becomes swollen and softened on the two surfaces, similar to a gelatinous cell-membrane ("callus"). This callus evidently serves to close the openings of the sieve-plate in the winter.[1]

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[1] See DE BARY, Comparative Anatomy. WILHELM, JANCZEWSKI, and other authors have carried on special researches concerning sieve-tubes.

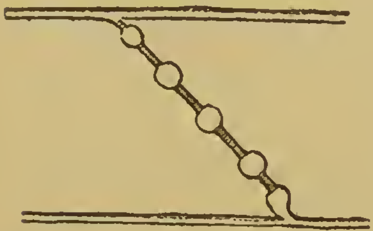
FIG. 43. — Septum of a sieve-tube with four sieve-plates.
(Diagramatic, after de Bary.)

The following table gives the earlier and later names of cell-forms which were included in the old expression "vascular bundle." It forms a fitting conclusion to the discussion of the cell-forms enumerated in this chapter.

HABERLANDT'S *Synopsis of Cell-forms, Slightly Modified by the Author.*

"*Vascular bundle*" of earlier authors			*Bast*	*Phloëm* (Nägeli)
	Mestome (Schwendener)	*Leptome* (Haberlandt) *Sieve-portion* (de Bary), unluckily named "soft bast" by some	*Sieve-tubes* and *conducting-cells*	
			Cambiform	
			Longitudinal bundle-parenchyma	
			Medullary-ray parenchyma	
		Hadrome (Haberlandt) *Vascular portion* (de Bary)	*Vessels* and *tracheids*	*Xylem* (Nägeli), usually called "wood."
			Woody parenchyma	
			Ray-parenchyma	
			Libriform	

Bast and *libriform* really do not belong to the "mestome"; they form (inclusive of collenchyma) an independent tissue-system, the *stereome* (mechanical system).

A small conducting system which is not widely distributed, but is limited to certain plant-families, has not yet been touched upon, but will now be briefly discussed. This is the *laticiferous* tissue ("milk-tubes").

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[1] DE BARY, Comparative Anatomy.

(*b*) *The Laticiferous Tissue.*

An important conclusion to the subject under consideration, that is, the cell-forms which conduct water and food substances, is the discussion of the milk-tissue or laticiferous tissue of plants. The laticiferous tubes occur most frequently, but not exclusively, in the albumen-conducting tissues of the vascular bundles; they are also found in the outer parenchyma and in some other tissues. This tissue-system affords an excellent illustration of the correctness of this statement: Different modes of development produce physiologically similar structures. There are: 1, *simple*, 2, *complex*, milk-tubes. In the mature state both present the appearance of a much-branched system of canals, though even in the earlier stages close examination will reveal the distinguishing characteristics of the two forms of tissues. The complex milk-tubes (*Cichoriaceæ*, *Papaveraceæ*) form a reticular structure by the joining of many branches ("anastomosing"); the simple (*Euphorbiaceæ*, *Apocynaceæ*, *Moraceæ*) tubes seldom anastomose, or perhaps not at all. To determine whether a given milk-tissue is simple or complex is one of the difficult problems of plant-anatomy, and conclusions differ with different authors.

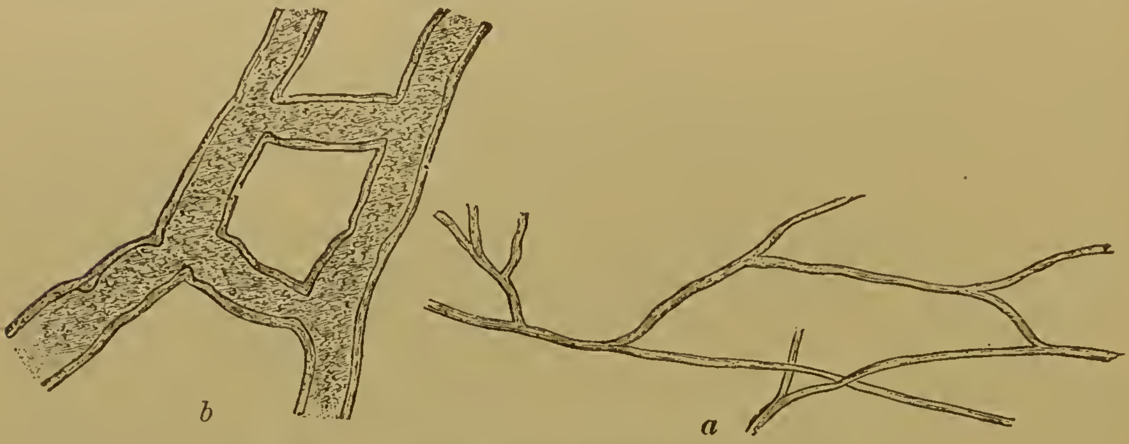

FIG. 44.—Laticiferous vessels (diagramatic).
a, Branching; *b*, anastomosing.

The names indicate the mode of development of the two forms of tissue. The complex milk-tubes are cell-fusions in which the remnants of the unabsorbed cell-walls are visible at the points of union (see Fig. 44, *b*). The simple forms can be traced to a few milk-cells which exist in the embryo of the plant, and which subsequently grow in length and branch in a manner similar to the hyphæ of fungi (Fig. 44, *a*). As already stated, anastomosing (fusion) rarely or never (?) occurs in the simple milk-tubes. There is nothing definitely known concerning the physiology and movement of the fluid within the laticiferous vessels. The following may, however, suffice to give an idea of the probable condition of affairs: The milky fluid is composed mainly of water, fats, starch, tannin, and grains of resin; it is usually white, more rarely yellow or red. Observations, even those of a purely comparative character, indicate that the milk-tubes obtain at least their carbohydrates from the centres of assimilation, namely, from the palisade-cells of the leaves. The fact that the milk-sap sometimes becomes watery, for example, when seeds germinate in the dark, would seem to indicate that it is a formative substance. In certain cases it has been observed that the presence of milk-tubes in leaves corresponded to a diminution of the conducting-parenchyma of the vascular bundle.

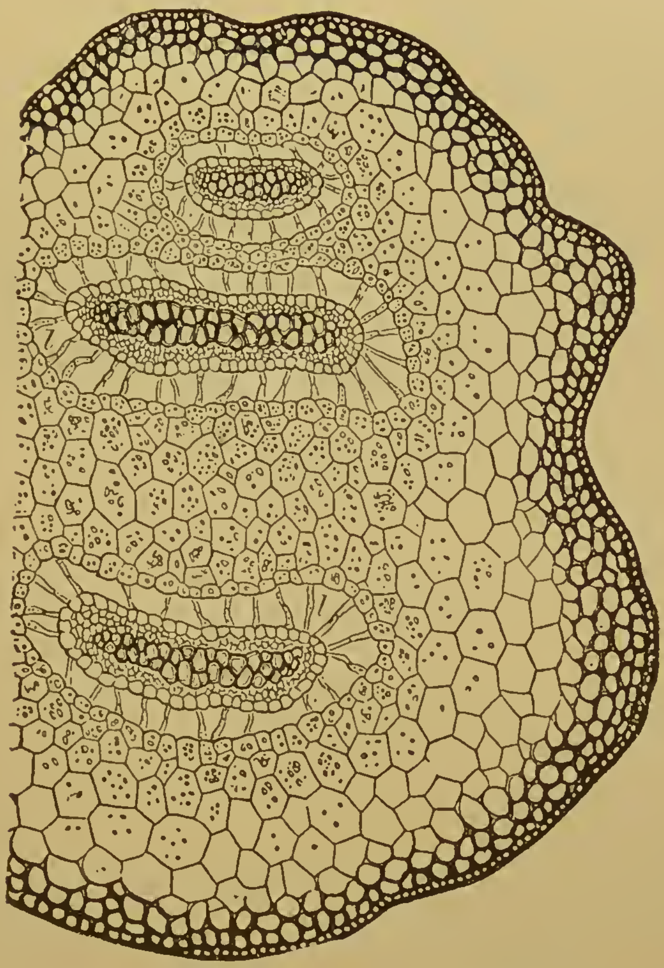

Fig. 45.—Cross-section of the stem of *Selaginella inæqualifolia*. (×150.) (After Sachs.)

In reference to the *movements* of the milk-sap we must make a distinction between thick-walled and thin-walled milk-tubes. In the latter it is essentially the *hydrostatic pressure of the surround-*

ing cells that causes the movement; in the former the elastic force of the walls themselves is brought into requisition (SCHWENDENER). Physiology leaves it an open question whether or not milk-sap also contains products which are useless in the further processes of nutrition. Milk-sap may also serve collateral functions. The sap escaping from injured tissues forms an air-tight protective coating. The questions relating to the function and use of milk-sap require further study, however.

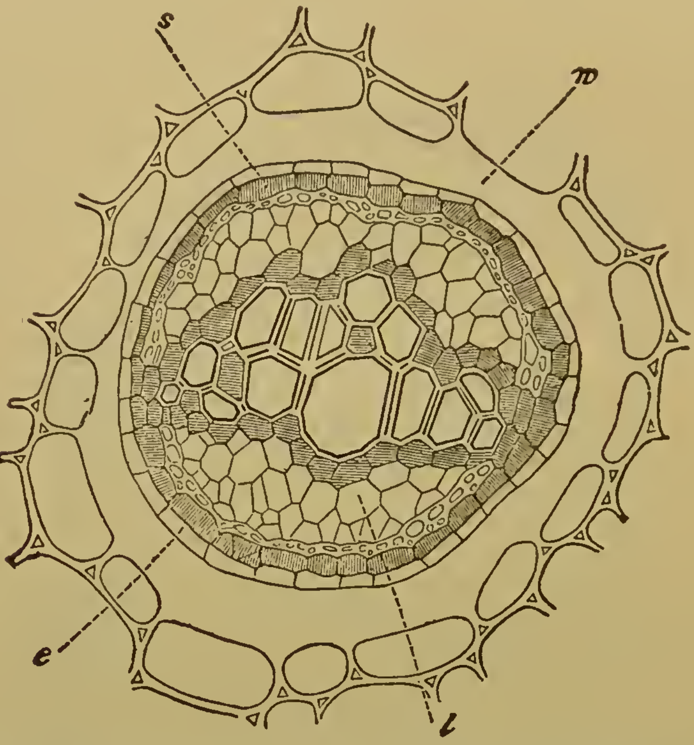

FIG. 46.—Smaller vascular bundle of the rhizome of *Polypodium glaucophyllum*. (After Potonié.)

Having now obtained a knowledge of the cell-forms, we shall next proceed with the anatomical (in part also the developmental) and physiological discussion of the chief plant-organs of the entire vegetable kingdom, beginning with the mosses.

(c) *The Stem-Structure of Mosses and Vascular Cryptogams.*

In the stem of mosses (example, *Polytrichum*) the central bundle of thin-walled cells represents the vascular system; a strictly peripheral ring of thick-walled cells functions as the mechanical system (HABERLANDT.)[1]

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[1] Beiträge zur Anatomie und Physiologie der Laubmoose, Pringsheim's Jahrbücher, 1886.

A cross-section of the stem of a vascular cryptogam (*Selaginella inæqualifolia*) may also serve to show the structural relations of the upright and semi-upright (hence more or less firm and elastic) stems of the fern-leaves.

Fig. 45 represents the peripheral mechanical ring of the stem. In the centre lie three vascular bundles surrounded by a loose connective tissue with large intercellular air-spaces. We can now also understand the structure of a single vascular bundle of a fern (see Fig. 46), which in many respects resembles that of *Selaginella.* The leptome in the form of two crescents lies in contact with the plate consisting of woody parenchymatous and tracheal elements; the fascicular conducting-parenchyma *s* surrounds the albumen-conducting elements in the form of a ring. The protective sheath is shown at *e*, the strengthening layer at *w*. I wish to state at this point that according to more recent investigators the majority of vascular cryptogams do not possess a true vascular system; the tracheal elements, in most cases, prove to be *tracheids*.

Furthermore, in the group of vascular cryptogams there is represented a wholly different type of structure; this type is well illustrated in the *Equisetaceæ.* For special functions, and hence explanatory from a physiological standpoint, the stem of *Equisetum* has an essentially different structure from the stem of *Selaginella* and the leaf-stems of related ferns. On account of the rudimentary leaf-development among the *Equisetaceæ*, assimilation on the part of the leaf is almost zero; only the toothed leaf-sheaths are present, and these function at the same time as mechanical structures. The stem with its branches must therefore perform the function of assimilation. To suit this requirement the mechanical and assimilating systems are alternately arranged on the outer surface. A glance at Fig. 47 will explain this arrangement. Between the bast-ribs (black) lie the assimilating tissues *gr*; inside of the bast-ribs are found the conducting bundles *L*, and between these the large intercellular air-passages. (This figure also illustrates the rare case of an inner and an outer "protective sheath," concerning which more particular mention will be made later. The dotted lines indicate their courses.)

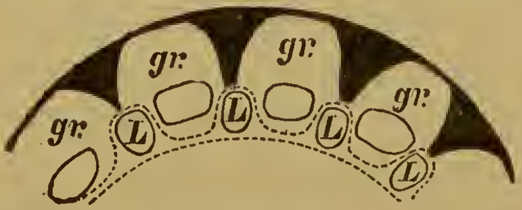

Fig. 47.—Transverse section of the stem of *Equisetum hiemale.* (Diagramatic.)

(*d*) *The Stem of Monocotyledons, Dicotyledons, and Gymnosperms.*

Elementary treatises on the stem-structure of the great divisions of *monocotyledons* and *dicotyledons* emphasize two distinctive characters, namely, that *monocotyledons* in general do not essentially grow in thickness, that their "closed" vascular bundles are scattered through the stem as seen in cross-section; on the other hand *dicotyledons* grow in thickness by means of a cambium and their "open" vascular bundles are arranged in the form of a ring, as shown in cross-section. Further investigations will of course reveal other differences.

The normal monocotyledonous stem is formed differently from the normal dicotyledonous stem. In the palm the young plant in its earliest stages of development forms a structure of considerable diameter; upon this the stem is subsequently elongated similarly to the building of a tower; a more or less embryonic condition toward the apex is not excluded. The dicotyledonous stem, for example—maple, grows to a considerable length during the first year; during the second year it adds to this length and also grows in thickness at the basal portion according to the mechanical requirements; that is, it has the ability to surround the stem of the first year's growth with a second annual ring; during the third year an additional ring is formed around the second year's growth, and so on for a number of years; therefore the base of the tree increases in thickness, and hence in strength, corresponding to the increase in height. (*Gymnosperms* grow in a similar manner.)

It is well to note the fact that the specific mechanical elements of dicotyledons and of monocotyledons are differently united with the conducting elements. In the latter the mechanical elements and the conducting elements are either entirely separated or are placed in juxtaposition.

The comparison of the two great plant-groups suggests still another thought. If one recalls the mechanical principles which underlie the arrangement of mechanical elements in the firm organs, and if we study a cross-section of an oak or conifer, the idea must suggest itself that rational constructive principles from a purely mechanical standpoint are wholly out of the question; for we have here, leaving out of consideration the small amount of pith, almost a solid cylinder of wood, and not a *hollow cylinder*, which is the type of a perfect mechanical construction. In fact, SCHWENDENER would probably not have succeeded in proving that dicotyledons as well as monocotyledons have a specific mechanical tissue-system. It must be remembered that in dealing with dicotyledons and conifers we are concerned with *living plants*, and not with dead models or types for mechanical engineers. The anatomist knows that the older rings, and hence a part of the inner mass of the wood (see heart-wood), at least up to a certain age, serve a wholly different function from that of pure mechanics; they contain living elements, namely, wood-parenchyma and medullary rays, which bear starch during the winter months. The function of *storing* reserve food-substances, concerning which more will be said later, is here of prime importance. Furthermore, since it is generally known that the woody plants of the geologic ages, as well as those of the present time, are of inestimable value to mankind, no one need hesitate in expressing the opinion that there is a general manifestation of a purposeful relation of the various organic kingdoms. Such relations are also observed in other domains.

Let us now proceed farther with the discussion of the anatomical differences between the monocotyledonous stem and the stem of dicotyledons as well as that of conifers.

The Arrangement of Vascular Bundles.[1]—In the monocotyledonous stem the vascular bundles lie *isolated* in the fundamental tissue; in the dicotyledonous stem they form a cylindrical mantle fused with the cambium. The apparent promiscuous distribution of the vascular bundles of monocotyledons must not be considered as being of any special importance: an arrangement in a series of circles, for example, is frequently noticed. We may designate as *fundamental tissue* (in partial agreement with SACHS) that which remains after the epidermal tissues, the mechanical and the conducting elements, have been removed; hence the tissue in which the mechanical and the conducting bundle-elements seem to be imbedded.

The individual bundle in the mature monocotyledonous stem has no cambium (long-celled prosenchymatous formative tissue) even at a very short distance from the primary meristem of the apex. The typical dicotyledonous bundle possesses cambium during its entire life-period. The elements of the vascular bundles of the monocotyledons also had their origin from cambium, but the formative tissue soon becomes changed into permanent tissue-elements, and in regard to the individual bundle this change proceeded centripetally; the sieve-tube tissue (leptome) and the vessel-bearing portion (hadrome) with the accompanying mechanical cells lie in close proximity. In dicotyledons and conifers the corresponding tissues—namely, the secondary cortex, which is formed outwardly by the cambium, and the wood, formed inwardly—are *always* separated by the cambium. In winter there is at least one cell-layer of the cambium, which represents the separating boundary between the cortex and wood. The cortex, which is formed from the first or primary meristem of the stem-apex, and which therefore existed before the appearance of the cambium-ring, is called *primary cortex*, in distinction to the cortex formed by the cambium. It does not show the characteristic radial structure seen in the secondary cortex.

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[1] Recent authors still use this expression in the same sense as did the older authors, namely, for tissue-bundles which consist of conducting elements as well as of mechanical elements.

The customary way of speaking of the monocotyledonous bundles as "closed" and those of dicotyledons as "open" is rather unfortunate,[1] for the monocotyledonous bundles are opened toward the fundamental tissue by means of special structural arrangements (transit-cells, large thin-walled cells, etc.), while the dicotyledonous bundles form a closed complex by means of the cambium, so that the individual bundle is scarcely recognizable as such. Therefore the fundamental tissue of dicotyledons and conifers is plainly divided into cortex and parenchyma (medulla), a peripheral and a central portion, which have an anatomical-physiological connection through the medullary rays. In monocotyledons the boundary-line between cortex and medulla is also often well marked, at least in the numerous cases in which the bast-ring represents the mechanical system. From some statements made by SCHWENDENER on p. 71 of his "Mechanische Princip" it would seem that such demarcation between the cortex and the medulla of monocotyledons without a bast-ring is not easily demonstrated. With regard to the radially diagonal course of many leaf-bundles in monocotyledons, SCHWENDENER has designated as cortex that peripheral portion in which the leaf-traces (the vascular bundles entering from the leaves) in their course downward extend diagonally inward or parallel with the outer surface. As a result the inner boundary of this cortex does not form a smooth, even surface: it is rather a cylindrical surface with numerous projections.

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[1] Nägeli designated the monocotyledonous bundles not as "closed," but as "enclosed," which is more nearly correct.

This leads to the discussion of the arrangement of vascular bundles in the stem and in other organs. We shall begin with the stem, and allude to the most important facts only.

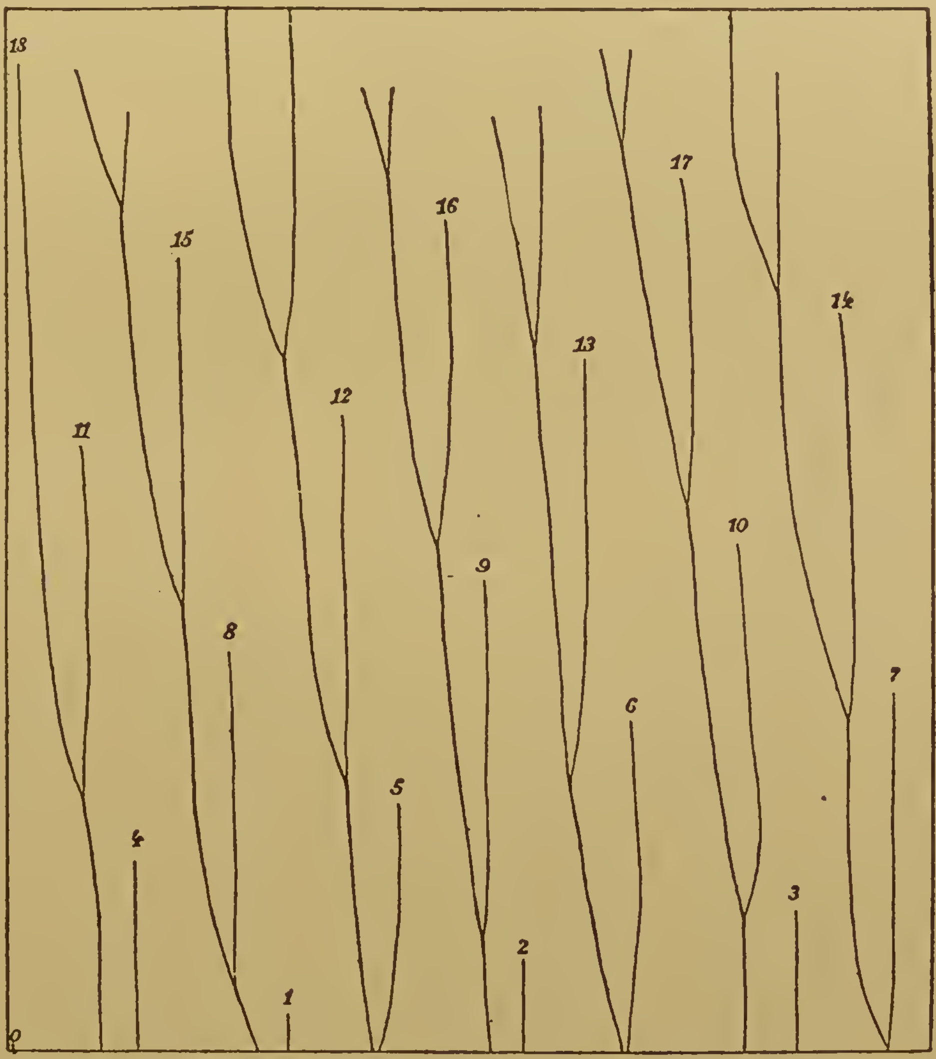

FIG. 48.—Arrangement of the vascular bundles in *Sedum reflexum*. (After Teitz.)

Each one of the spirally arranged leaves appears with its vascular system, as indicated by the numbers. This figure also has a bearing upon the subsequent discussion of the mechanical influence which the position of mature leaf-bundles in the stem has on the position of young leaves.

Among dicotyledons the leaf-bundles usually extend radially vertical. In most monocotyledons the numerous leaf-traces of each leaf do not all take the same course. The median leaf-bundles extend most deeply into the stem, describing a curve upon the radial plane; those bundles placed in a somewhat more lateral position penetrate less deeply and describe a smaller curve; those still more lateral enter least deeply and soon extend vertically downward. In monocotyledons the course of the vascular bundles in the tangential plane may be described as follows: *Each radially curved bundle inclines in a tangential direction.* Among dicotyledons a tangentially inclined course of the vascular bundles is the rule; they unite laterally after they have taken an isolated course downward for some distance. Fig. 48 represents the tangentially inclining course of the leaf-bundles of *Sedum reflexum* (dicotyledon) upon the surface of a cylinder.

There is a leaf at every node and every leaf contains vascular bundles. The radially diagonal course of the vascular bundles in monocotyledons is shown in Fig. 49, which is a diagramatic median longitudinal section. Only a few of the leaf-bundles are represented in order to illustrate the relations explained above. The dotted lines are intended to show the tangentially inclined course of the radially curved bundles. The arrangement and distribution of vascular bundles, according to the requirements of nutrition, that is, for the uniform distribution of water and of food-substances, have received special attention from HABERLANDT.[1] The numerous anastomoses of vascular bundles in the leaves are of great importance in cases of local injury, in that the neighboring bundles are thereby enabled to take up the work of those destroyed. (The circulatory system in man is similarly arranged.)

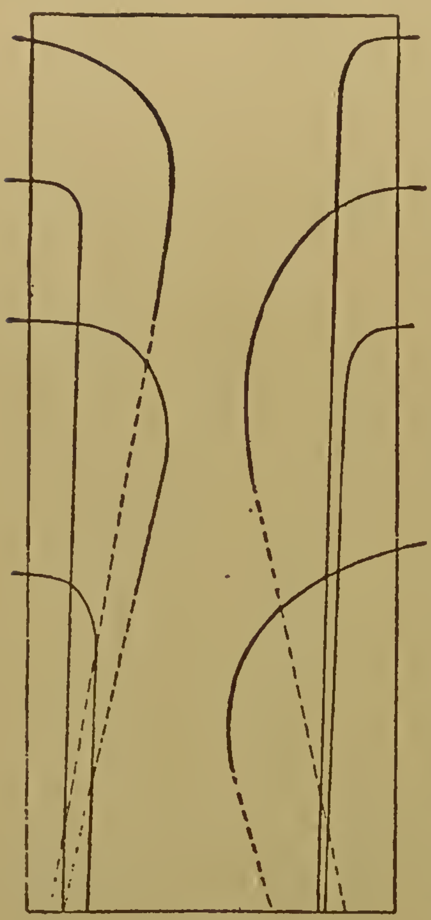

FIG. 49.

The following is of importance in regard to the *arrangement* and *structure* of the vascular bundles in the *leaves*. Green leaves are for the purpose of assimilation. Therefore the *mechanical* elements must maintain these flattened organs in a suitable position with regard to the light (see pp. 67 and 68 in regard to the mechanical tissue—bast—of the vascular bundles); the *conducting* elements must on the one hand carry the necessary water and the various food-substances to the leaves, and on the other hand they must conduct the products of assimilation from the leaves to the stem. As we have already learned, the leptome in the stems of monocotyledons and dicotyledons is placed toward the outer surface, the vascular portion toward the interior; corresponding to this arrangement we find the leptome of the leaves near the lower surface and the hadrome (vascular portion) near the upper surface. Occasionally skeleton-bundles (mechanical cells) which prevent the tearing of leaves by strong winds, etc., are brought into mechanical operation; these bundles are usually found near the middle of

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[1] Phys. Pflanzen-Anatomie.

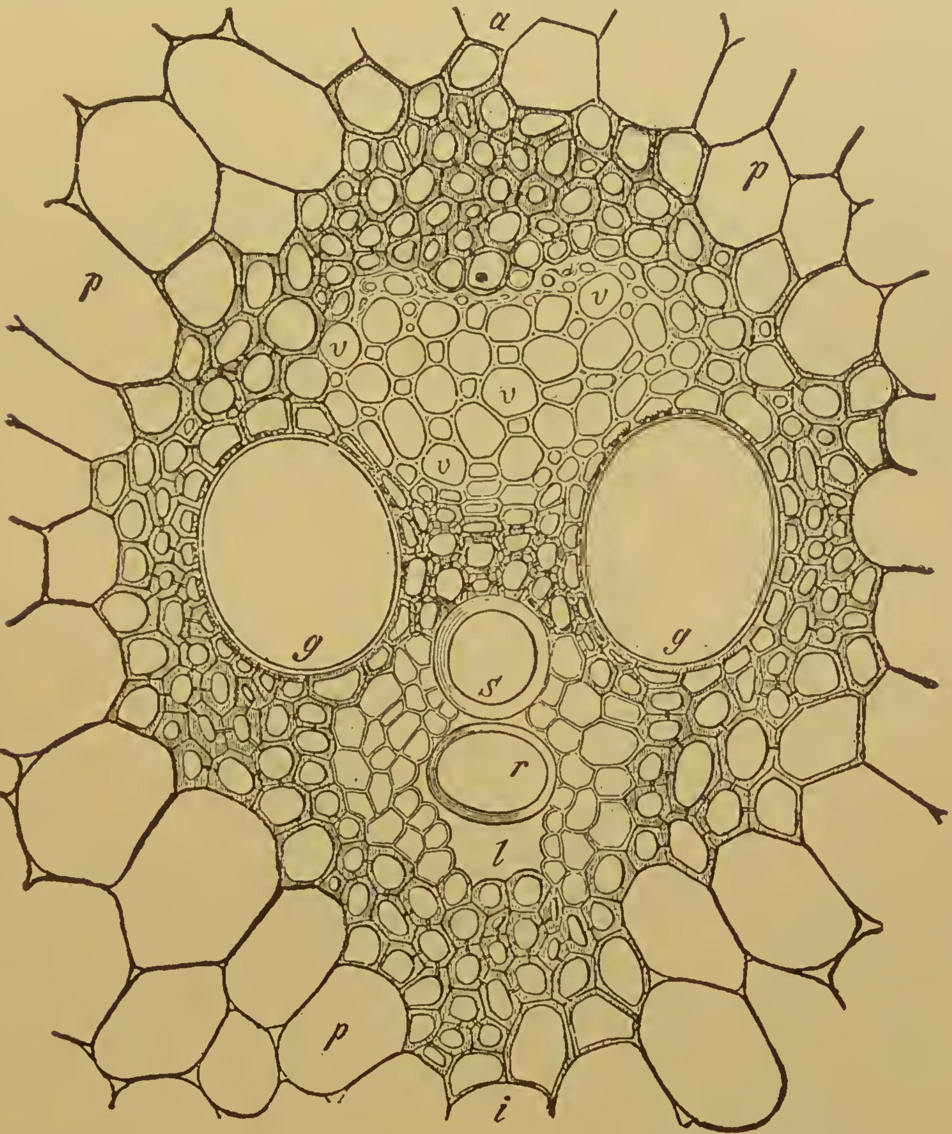

FIG. 50.—Vascular bundle of the stem of *Zea Mays*. (× 560.)

v, Albumen-conducting tissue, *leptome* or *sieve-tissue*; *p*, parenchyma; *s* and *r*, primordial (primary) vessels; *g*, secondary vessels; *l*, intercellular space; *a*, side facing outward; *i*, side facing inward. (After Sachs.)

the leaf, as seen in cross-section. Further, there are often special mechanical cells at the margin of the leaf which also assist in preventing tearing (Sachs, Haberlandt, Hintz).

Although the difference between monocotyledons and dicotyledons is very great, we must not omit to note the similarities that exist. If we leave out of consideration the cambium, we cannot fail to see the similarity between a monocotyledonous and a dicotyledonous vascular bundle. The explanations of the figures of the monocotyledonous bundles in the text-books of Sachs, Haberlandt, Frank, and in the plates of Kny, are imperfect, since the rather plentiful wood-parenchyma is scarcely, or not at all, mentioned. The tissue between the two large vessels (g) and the ring-vessels (s, r in Fig. 50), near the sides between the two larger vessels, are in part wood-parenchyma, in part thick-walled

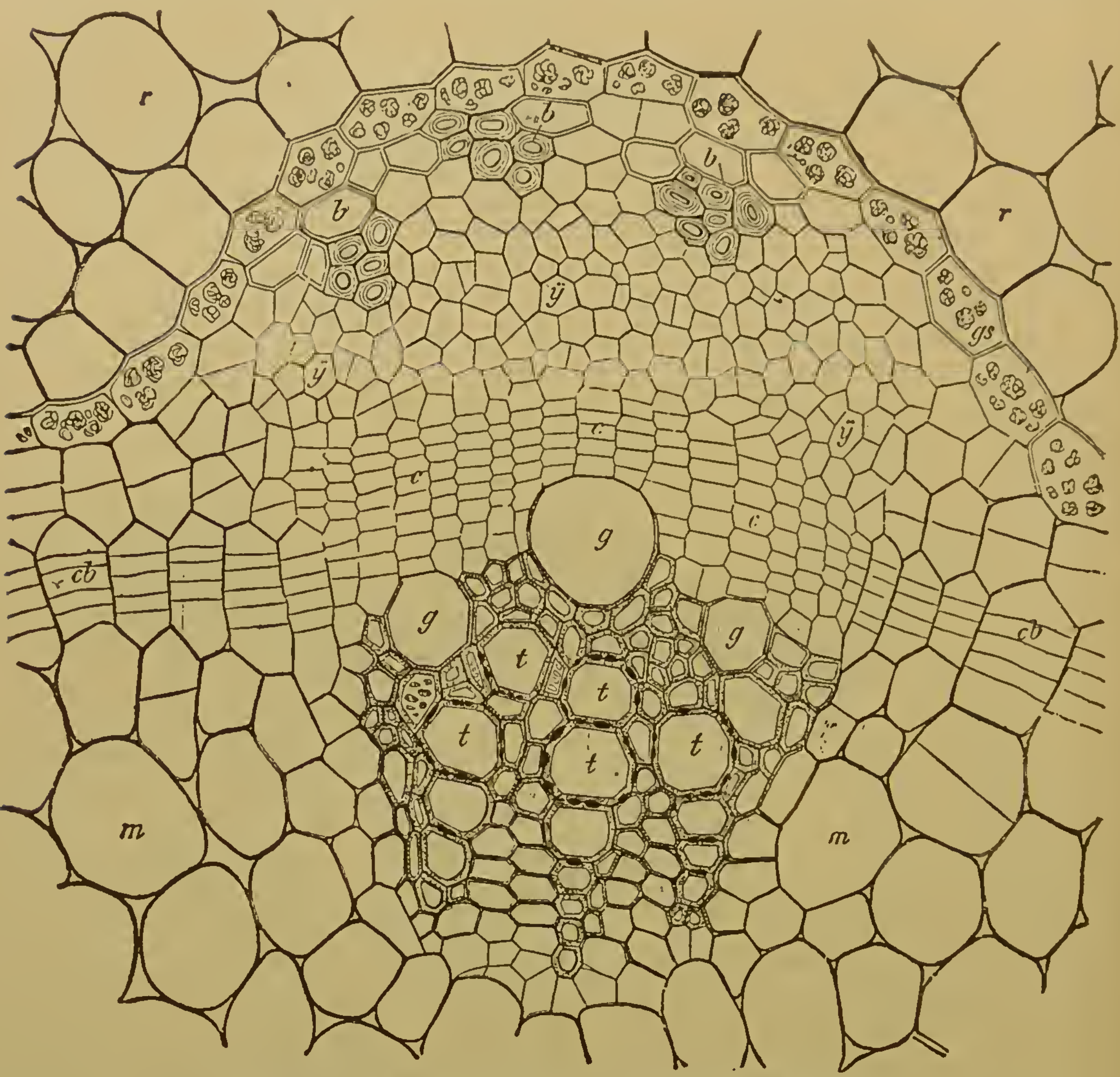

Fig. 51.—Vascular bundle of *Ricinus communis*.
b, Bast; y, sieve-tissue or leptome; g and t, vessels; c and cb, cambium; r, parenchyma; just beyond b a starch-bearing layer (bundle-sheath). (After Sachs.)

and in part thin-walled tissue. In both monocotyledons and dicotyledons (see figures) an imaginary line drawn through the stem in cross-section first cuts the outer bundle-elements of the albumen-conducting tissue, next the two secondary vessels and the wood-parenchyma, and finally, still more internally, the primordial vessels and the thin-walled wood-parenchyma. In both plant-divisions the primordial vessels are narrower than the secondary vessels. The mechanical cells of the vascular bundle of *Zea Mays* leave four passage-ways between the fundamental tissue and the interior of the bundle. The accompanying diagramatic figure (52) shows this much better than the figure of the vascular bundle of *Zea Mays*, in which the four passages are scarcely recognizable. They are indicated by an increase in the size of the cells. Since the mechanical (skeleton) cells in general do not belong to the conducting bundle, we find that they are not present in the hadrome of the *Ricinus*-bundle, but are arranged in small groups near the leptome. In this respect, however, the bundles of the dicotyledonous stem differ very frequently.

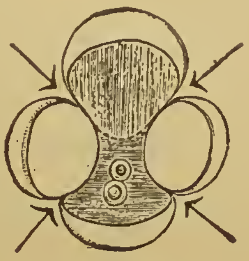

FIG. 52.
(Diagramatic.)

(*e*) *Growth in Thickness among Dicotyledons and Monocotyledons by Means of the Cambium.*

It is important to recognize the fact that the cambium of our endogenous trees and shrubs is a *bipolar* formative tissue; that is, each individual normal cambium-cell, when at the height of its activity, must show: 1, a daughter-cell which was cut off outwardly; 2, a daughter-cell which was cut off inwardly; and 3, a cell lying between the two having the power of again dividing. These middle cells (3) form a cylindrical covering (cambium covering) in the stems and roots. In cross-section this appears as a ring.

Growth in thickness of stems and roots by means of the cambium-ring produces such characteristic structural changes as will astonish the young anatomist in the examination of cross-, tangential, and radial sections. He will also observe numerous deviations from the normal growth-type. To enter into a more particular discussion of these deviations is impracticable, though it is necessary to bear in mind that they exist. We shall now enter into a brief discussion of the characteristic activity of the cambium-ring and the typical appearance of various sections of stems and roots.

A *cross-section* shows the successive order of the products resulting from the cambial activity, namely, the arrangement of the wood-elements on one side of the cambium, and the secondary cortex on the other side. *Radial bands* can be traced from the wood through the cambium into the albumen-conducting tissue. It should be noted that the primordial arrangement is, for various reasons, very materially altered at some distance from the cambium (hence at a later period). This secondary change consists mainly in an increase in the size of the elements (gliding growth, KRABBE), and in subsequent divisions of the leptome-elements. As a rule, the radial structure is most distinctly shown in *conifers*. The cause for this can readily be explained. Elementary anatomy teaches that *vessels* are wanting in the wood of conifers. Macroscopical examination of cross-sections shows this in the absence of the large vascular lumina; microscopically this is evident by the large regularly arranged woody elements (tracheids and medullary rays). Wood-parenchyma is rarely present. The following elements bring about a change in the anatomical appearance: 1, resin-ducts; they usually extend longitudinally in the sparingly present wood-parenchyma, or they may extend radially in the medullary ray tissue; 2, the difference between the growth-products in the *spring* and in the *autumn*.

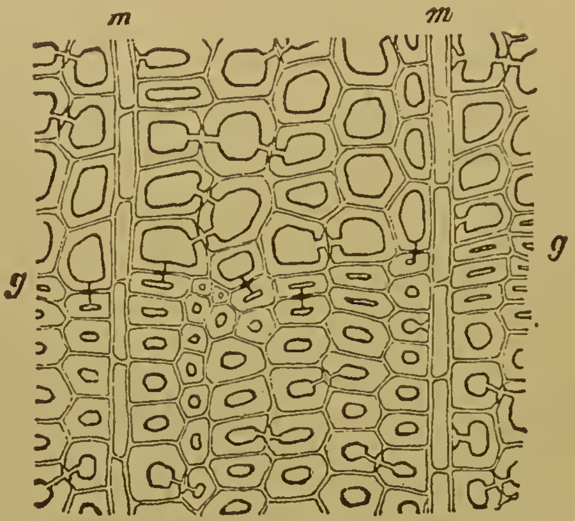

FIG. 53.—Woody tissue of *Taxus baccata* (cross-section). *g*, Limit of the year's growth; *m*, medullary rays. (After Haberlandt.)

The latter morphological factor (2) has a bearing upon coniferous wood as well as upon dicotyledonous wood, and will receive our immediate attention. *Apparently* radially compressed, narrow-lumened, thick-walled elements mark off the autumn-wood or summer-wood. On the other hand wide-lumened, thin-walled, radially elongated, or, at least, not radially shortened, cell-forms belong to the spring-wood. Among angiospermous trees this contrast is strongly marked by the minuteness or absence of vessels in the autumn-wood as compared with the large size and great numbers of the same in the spring-wood. This difference, which is usually visible to the naked eye and which marks off the *yearly* rings, is

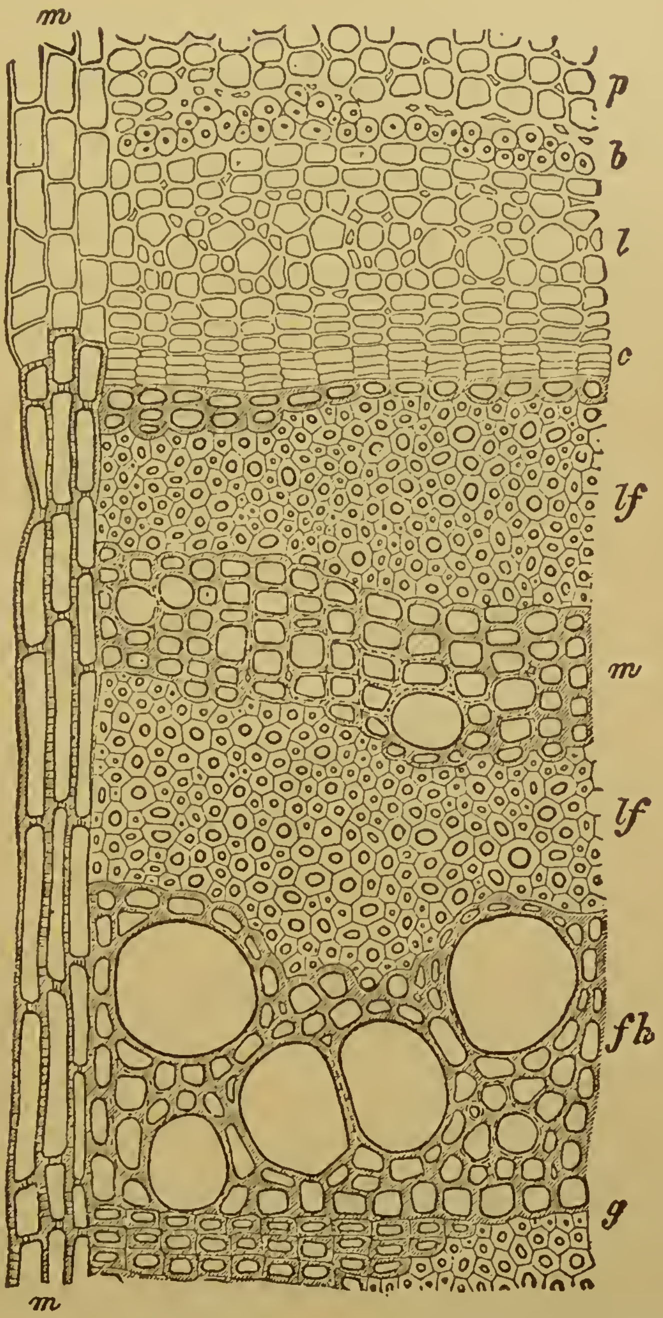

FIG. 54.—Section of a ring of the previous year's growth. *Cystisus Laburnum.* *m*, Medullary rays; *p*, secondary bark-parenchyma; *b*, bast; *l*, leptome; *c*. cambium; *lf*, libriform tissue; *m*, mestome; *g*, year's limit. (After Haberlandt.)

supposed to be due to an increased cortical pressure in the fall of the year (Sachs, de Vries). This assumption can no longer be maintained in the light of present knowledge of physiological science.[1] Even if we were concerned only with apparent transformations due to pressure, namely, tangential spreading, or radial flattening, this hypothesis would not be tenable, because of the fact that radial pressure, in the fall, increases only slightly or may even diminish. However that may be, it is evident that the final decision as to whether a given cambium-cell will develop into libriform, wood-parenchyma cell, or a vessel with its characteristic thickenings of the walls, cannot simply depend upon a greater or lesser pressure exerted by the cortex. Krabbe in his first publication referring to this subject questions rightly: "Is the vessel perhaps a large libriform-cell, or is it, *vice versa*, a small vessel?" The annual rings are not equally distinct in the different trees and shrubs.

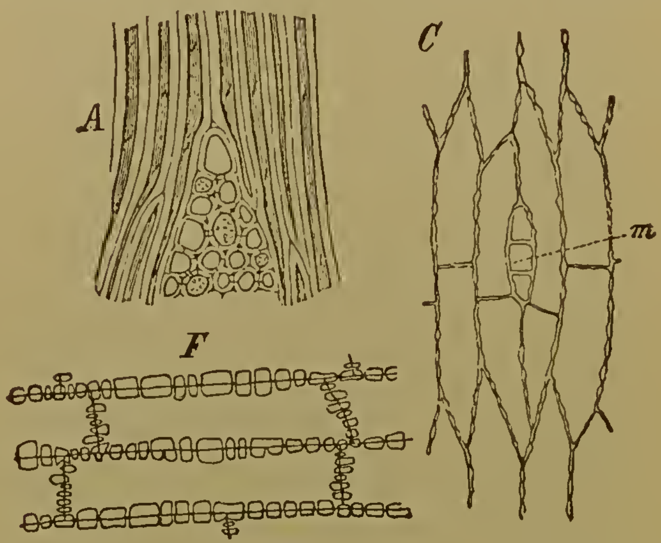

Fig. 55.—Medullary rays of *Cystisus Laburnum.*
A, Large and *Cm*, small medullary rays in tangential longitudinal section; *F*, ray in radial longitudinal section. (After Haberlandt.)

A *radial longitudinal section* of dicotyledonous or coniferous wood in surface-view must of necessity show, scattered here and there, the medullary rays whose elements always cross the longitudinally extending elements at right angles. I can only point out the fact that cells bearing a resemblance to tracheids form the medullary rays of some conifers. The length of the medullary rays, their size and the number of cells in transverse direction, the origin of a ray in the medulla and in the primary cortex or at some distance from them ("primary" and "secondary" medullary rays), the direction of elongation (stretching) of the cells, etc., produce many changes in the appearance of the plant-structure. These and similar anatomical characteristics are also of special interest to the palæontologist in determining the probable systematic position of fossil-plants. Sometimes the connection between medullary ray-tissue and wood-parenchyma is very distinct and forms a system, when, for example, the wood-parenchyma cells form transverse connecting-bands between the medullary rays. There is another phenomenon which is of frequent occurrence and which must receive special mention, though its significance has only been approximately determined from a physiological standpoint, namely, that the dead tracheal system and the living cells (medullary rays and wood-parenchyma) form such an intimate anatomical relationship as to enable the interchange of fluids between them (assisted by the cell-pores). Further, we notice an *increase in the length* of the mechanical elements of the woody body in a direction from the younger rings to the older rings (hence from without inward). Upon this perhaps depends the apparent torsion of stems, that is, the tangentially slanting arrangement of the woody elements.

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[1] Compare Krabbe, Uber die Beziehungen der Rindenspannung, etc., Sitzungsber. der Berl. Akad., 1882. Also Krabbe, Über das Wachsthum des Verdickungsringes, etc., Abhandl. der Berl. Akad., 1884.

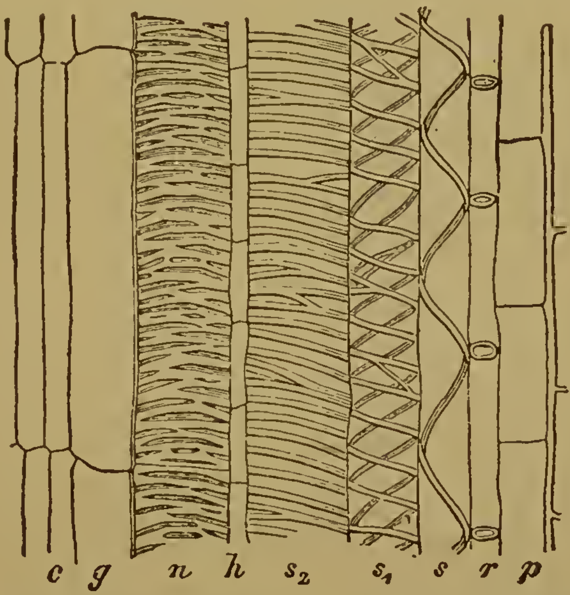

FIG. 56.—Radial longitudinal section of the vascular bundle in the stem of *Œnothera odorata*.

c, Cambium; *g*, primordial vessels. The different forms of vessels will be recognized from previous descriptions. (After Haberlandt.)

In regard to the vessels, a radial longitudinal section shows the variable structure of the perforated transverse septa (remnants of the cell-walls); they may be scalariform, reticular, or annular. Tracheids have bordered-porous slanting end-surfaces; this is because the originally transverse septa in the stem incline to the right or left. Fig. 56, which represents a longitudinal radial section of a dictyoledonous stem one year old (*Œnothera*) illustrates the important difference between vessels which have grown in length with the other tissues and those which began development at the close of the vegetative period. Similar anatomical relations also exist in the innermost annual rings of the dicotyledonous stems.

A tangential longitudinal section again shows the characteristic appearances of the medullary rays. They appear as *two-edged* cell-rows or cell-groups, or as bands of cells of one or more layers in thickness, when the ends are invisible. The typical appearance of medullary rays in both longitudinal sections (radial and tangential) is as marked in the secondary cortex as it is in the wood.

The difference between *splint-wood* and *heart-wood* in dicotyledons and conifers has long been recognized. The variously colored woods of commerce always represent the heart-wood of the trees from which the wood has been taken, that is, the *inner* annual rings, which are usually very numerous. Splint-wood is from the younger tissue, therefore from the *outer* layers. The heart-wood is of a darker color than that of the splint, due to a coloring substance deposited in the cell-wall. Besides the coloring materials, tannin also is found in the cell-walls of the heart-wood. The lumina of the vessels and tracheids are either closed by a hardened gum ("heart-gum"), more rarely by a resin, or by cells (tyloses), which latter grow through the pores from the immediate vicinity. These changes render the heart-wood functionless as far as the conduction of water and the storing of carbohydrates is concerned, but it is on the other hand less subject to decay. The latter property and especially the occlusion of the vessels, makes such heart-wood formations especially important, because they serve as a protective coating not only to the inner portions of the stem, but also to external injuries; for example, on the cut or broken surfaces of stems and branches there is formed a resinous or gummy protective covering; hence the name "protective gum" or "wound gum" (callus) (FRANK).

I may only mention the interesting "*overflow*" growths which proceed from the cambium in the case of injuries. Literally speaking, the cambium at the margin of the injury overflows with callus-parenchyma cells and callus-cortex, gradually covering the injured surface; finally the callus-tissues meet and the cambial layers again form a closed ring.

The annual rings in the cortex are not so definitely marked as they are in the wood-tissue. But because of the fact that the secondary cortex receives an additional layer from the cambium each year, it is not surprising that such annual rings should appear. The annual layer deposited on the outer surface of the cambium is, however, usually very thin, as compared with the layer deposited on the inside. It often happens that there are periodical deposits of thick-walled bast-cells formed. Observation shows, however, that such layers do not agree exactly in number with the annual rings of the wood.

By way of comparison of the *mechanical* and *conducting systems* in the monocotyledonous and dicotyledonous stems, the following may be added, though it is in part a repetition:

Among monocotyledons the mechanical system has its seat either in an independent simple or ribbed bast-ring, with which the conducting bundle (mestome) may be more or less intimately associated, or in a ring or wreath of isolated bast-bundles, or in strong bast-linings which accompany the conducting bundles.

In the majority of dicotyledonous stems the mechanical system is found within the cambium-ring of the woody tissue—"intracambial libriform ring." Among dicotyledons, in general, the mechanical system with its elements "penetrates" the mestome, that is, the conducting system.

Among dicotyledons there are instructive instances in which a bast-ring or a ring of bast-bundles gives the stem the required firmness during its early life-history. Later the mechanical support is transferred to the gradually increasing woody cylinder, while the above-mentioned bast-complexes are gradually displaced by bark-formations (*Berberis*, *Lonicera*, *Platanus*, *Betula*, etc.).

It may be mentioned here that there are monocotyledons (example, *Dracæna*) which have a secondary growth in thickness by means of a ring of meristematic tissue. In the case of *Dracæna* we have to deal with fibrous tracheids (similar to those of conifers), which are formed inwardly and united with the leptome in the form of bundles.

Now we have the opportunity to offer some suggestions in regard to the so-called

(*f*) "*Abnormal Structure of Stems.*"

The term "abnormal" is only meant to signify that stems (and ultimately also the roots of the plants concerned) of certain plants as compared with the stems of the majority of species indigenous to our northern hemisphere have peculiar structural conformations. The complex woody cylinder of *Sapindaceæ*, the peculiarly lobed or fissured stem of *Bignoniaceæ*, belong here. From the fact that we are concerned with a group of plants closely related by certain life-processes,—a *biological group*, so to speak,—nearly all of which are climbing or twining plants representing various families, the term "abnormal" is scarcely justifiable. Neither do we consider a climbing plant occurring in a group of non-climbing plants as abnormal. The following marks characterize the abnormal anatomical structure: reduced diameter of the stem; diminution of the loose medullary tissue, especially of the central medullary canal; centripetal tendency of mechanical elements; loculose structure of the woody portion, due to the presence of the elongated, frequently broad, medullary rays, and especially to a transfer of the *leptome to the woody body; large diameter* of vessels and sieve-tubes. There are reasons to suppose that the prevailing tendency of the growth in length of the plants under discussion, and the mechanical adaptations to resist torsions and pulling tensions, are the result of their habits as climbers, though the researches in regard to this subject are not conclusive.[1] Other so-called abnormal types are also very probably phenomena of specific adaptations; for example, in the autumn Begonias very frequently show the presence of vascular bundles in the fundamental tissue, etc. This subject requires further study, although sufficient has been said to indicate that the term abnormal as applied to the above instances has the same meaning as it would have if applied to aerial roots, since they also have a special adaptive structure. It is, however, very evident that aerial roots are strictly normal for the life-processes of the plants concerned.

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[1] Concerning this subject there is a study by Ambronn and myself in Flora, 1881. Further investigations by Schenk, Beiträge zur Anatomie der Lianen. Jena, 1893. Also my own publications in regard to *Begoniaceæ* and *Campanulaceæ*, Flora, 1879, and Monatsber. der Berl. Akad., 1881.

(g) *The Structure of Roots.*

The noticeable difference between the internal structure of roots and stems suggests the question: What are the physiological causes which produce such a difference? Only since SCHWENDENER's physiological studies of tissues have we been enabled to give an approximately correct answer to this question. According to the requirements of mechanical tension, we find a central arrangement of the relatively firm elements (see discussion of mechanical tissues). This centripetal tendency of mechanical elements governs the arrangement of tissues in the root; the absence of a medullary tissue, or at least the reduction of the same to a minimum, is thereby readily explained (teleologically, not causal-mechanically).

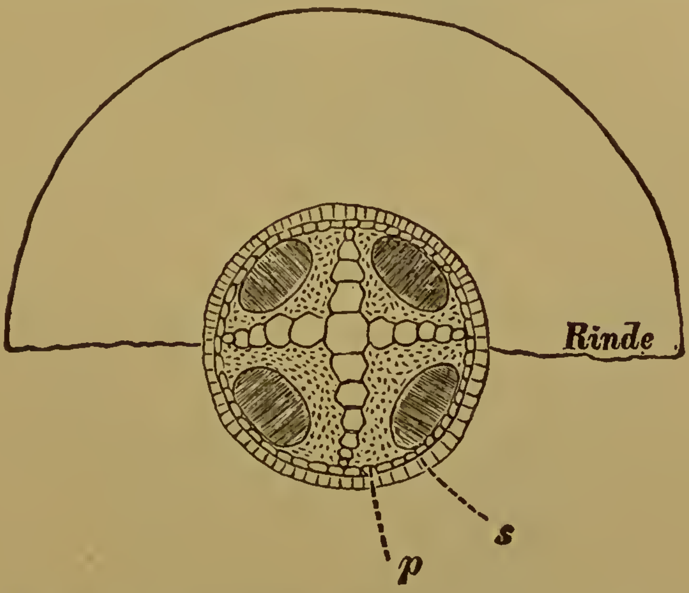

FIG. 57.—Cross-section of the root (diagramatic).

s, Bundle-sheath; *p*, pericambium. The root is "tetrarch"; between the four vascular bundles and the four groups of sieve-tissue lie the wood-parenchyma and the mechanical cells.

The fact must not be overlooked that the older and more centrally located root-portions serve primarily for the conduction of water, while the root-tip portions are specially qualified to take food substances from the soil. This predominating conducting function of older root-portions requires anatomical adaptations which are most suitably met by the compact, narrowed, central vascular bundle. It is known that the primary cortex very often loses its leaves, in which case there is in reality only a central bundle remaining. Leaving the root-cap out of consideration for the present, there are *three anatomical differences* between the root and the stem. These differences are as follows.

1. The *central* arrangement of the conducting elements and the mechanical elements in the root; their more peripheral arrangement in the stem.

2. The *centripetal* development of primordial vessels in the root; their *centrifugal* development in the stem.

3. The *tangential* arrangement of the two conducting bundle-portions, that is, the leptome and the hadrome (sieve-portion and vessel-portion), in the root; their radial arrangement in the stem.

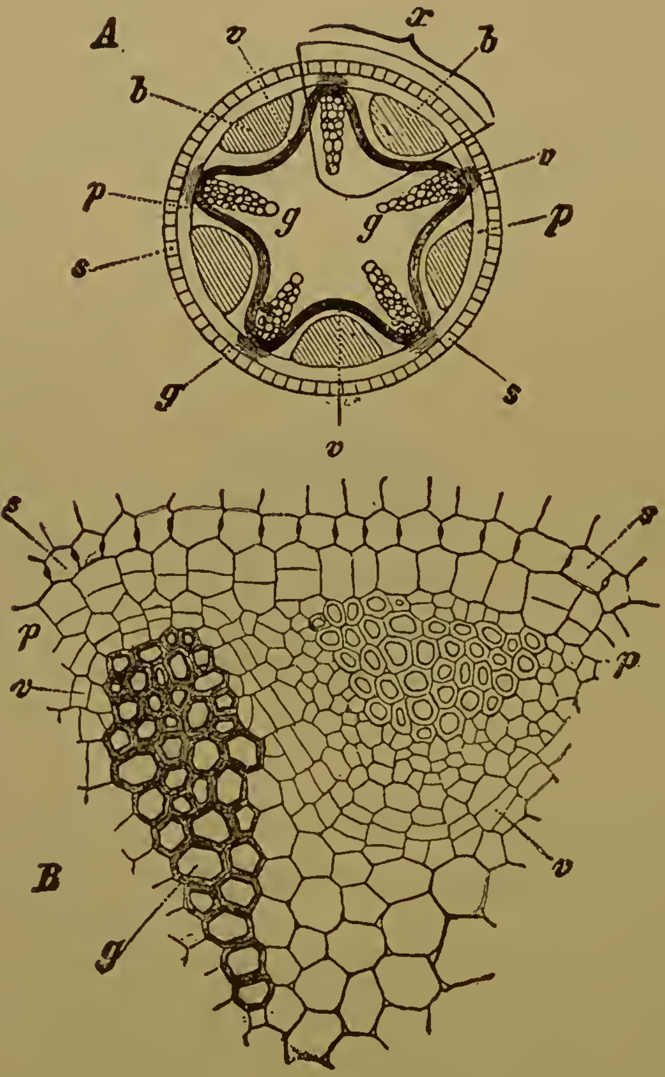

FIG. 58.
A, Diagramatic; *B*, anatomical representation of the segment x. (After Haberlandt.)

Ad 2. This anatomical characteristic is perhaps closely related to the first, in that its purpose seems to be to utilize the central space as much as possible. This arrangement is also advantageous in that it brings the vessels nearer the root-hairs which absorb the moisture from the soil. The vessels first formed (primary vessels) are somewhat scattered through the root, as seen in cross-section.

Ad 2 and 3. The number of vascular bundle-groups (hadrome-bundles) corresponds to the number of leptome-bundles, and according to this numerical relation roots are designated as "diarch," "triarch," "tetrarch," etc., "polyarch." The latter, that is, many bundle-groups, occur most frequently among monocotyledons; the former ("diarch," "triarch," etc.) are more common among dicotyledons. This anatomical relation is perhaps the reason why secondary growth in thickness cannot take place in the roots of monocotyledons, since the numerous primordial bundles require *eo ipso* a maximum circumference for their maturation. Among dicotyledonous roots secondary growth in thickness occurs frequently. As is well known, conifers and other trees often have roots a foot or more in diameter.

How do such roots grow in thickness? Fig. 58 represents the period at which secondary growth in thickness begins. The meaning of the letters are clear, with the exception of *v*, which indicates the cambial tissue. Tangential walls are formed within the sieve-tube bundles; cell-divisions continue along the sides of the bundles; finally, this process also begins immediately outside of the primordial vessels, upon which the cambial ring is completely closed. During the earlier stages this ring is two, three, or more lobed or loculose; later, when the secondary wood-formation has begun within the primordial albumen-bearing tissue, it becomes circular. In general, this cambium behaves like that of the stem, forming woody elements (wood-parenchyma, medullary rays, vessels and tracheids) inwardly, leptome and ultimately mechanical bast-cells outwardly. Thus, finally, the root can only be distinguished from the stem by the structure of the organic centre; in the root this must show a central tissue of three or more radiating primordial vessels instead of the medulla. Later the primordial leptome of the numerous conducting bundles is no longer found in the centre; it is crowded toward the periphery by the formation of the woody tissue. According to the above, there are certain portions of the pericambium *p* which take part in the formation of the cambium-ring, namely, those cells which lie above the vessels first formed. The bundle-sheath *s* (protective sheath) must either grow with the increase in thickness of the bundle or rupture. Such growth in the bundle-sheath has actually been observed. Should the central portion be wanting, it would be difficult to decide definitely whether the given wood belonged to a root or to a stem (a difficulty encountered by palæontologists).

Fleshy roots[1] (turnips) owe their condition, as a rule, either to the prevalence of the parenchyma (longitudinal parenchyma and ray-parenchyma) in the woody body or to the extensive development of the secondary cortex.

"Abnormal" root-structure is to be considered from a standpoint analogous to that of the stems referred to above.

(*h*) *Anatomy of the Transition-zone between the Stem and the Root.*

The question as to how the existing differences between the root and the stem become equalized at the transition-zone must force itself upon every anatomist who has studied the stem and root. Evidently the elements which conduct water in the roots continue the same function in the stem; hence it must undergo its typical transformation into stem-structure at a region near the surface of the soil. The description given by DE BARY[2] (after STRASBRUGER) of the case of *Biota orientalis* is simple and explicit. The student can easily study the transition-zone in longitudinal and cross sections.

The hypocotyledonous stem contains two bundles in its upper part, which extend perpendicularly downward from the two cotyledons; the bundle of the main root is diametrically diarch. In each of the two cotyledonous bundles the phloëm (leptome) divides into two equal parts near the base of the cotyledons. The leptome-halves diverge more and more, and are finally in the same tangential plane with the hadrome-group. Each one of the sieve-tube groups approaches a corresponding group from the other bundle and unites with it to form a broad leptome-group. The elements of both *portions* of the vascular system (leptome and hadrome) undergo a similar displacement or torsion at the same level of their course; so that

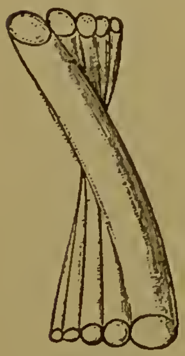

FIG. 59.

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[1] WEISS, J. E., Flora, 1880; also other authors.

[2] Comp. Anatomy, page 386. Also DODEL, Pringsheim's Jahrbücher, VIII.

the innermost (primitive) vessels incline most strongly toward the outside, the next following less strongly, etc. The accompanying figure (59) represents the latter displacement for the left side.

A certain regularity also exists in the union of the bundle-elements of root-branches with the corresponding elements of the main root. Without entering into the particulars of these and similar structural relations, we will direct attention to the fact that, in the majority of cases, the outer angle of a *vascular plate* of the main root is that to which the secondary vascular system becomes united. The vessels of both roots unite; the leptome-groups are derived from the immediate vicinity.

(*i*) *The Special Physiology of the Movements of Food-substances and Water in Plants.*

The *paths* in which, and the *forces* through which, water and food-substances are moved will next claim our attention.

Movement of the above-mentioned substances must take place. Carbohydrates, especially starch, must be transported from the places of formation to the centres of nutrition, and eventually to the storing tissues; and again from the latter to the centres of nutrition: or, in other words, from the green assimilating organs to the tubes and stems, to developing roots, flowers, seeds, etc., and from tubes and other storage-tissues to the places of organ-formations, such as the root-tip, the apical area of the stem, etc. Further, the organs of great surface-expansion (leaves) require a large quantity of water, for purely physical reasons (on account of evaporation), which must be conducted upward from the roots.

α. Conduction of Albumen.

Investigations concerning the seat of *albumen*-formation (Frank, Schimper) have perhaps already proceeded so far as to show that every living cell (not only the green ones) which contains *nitrates* and a corresponding C-bearing substance may be considered as a centre of amide-formation, and secondarily also of albumen. (Plasm is an essentially albuminous substance.) We, however, at once meet with difficulties in trying to explain the circulation of albuminous substances. Some uncertainty has recently arisen as to whether the sieve-tube tissue should be considered as albumen-

conducting or as albumen-*storing* (Frank). From the anatomical structure of sieve-tubes we may, however, safely assume that they are qualified to permit the mass movement of undissolved albuminoid substances (see above). The old and well-known girdling experiments teach that the substances necessary in the formation of organs, that is, albumen and carbohydrates, are checked in their course when the entire bark is removed. The question whether the two plastic substances each require a special path, that is, primary cortex for the one and secondary cortex (leptome) for the other, or whether the conditions are otherwise, is still unsettled. Frank is inclined to assume that the primary and secondary cortex, *without* the sieve-tubes, is chiefly employed in the conduction of carbohydrates and amides (the latter are considered as circulatory forms of albumen). The opinion that the contents of the sieve-tubes (especially albumen) are essentially serviceable in the *cambium* for the formation of tissues is doubtless correct, but it seems in exact opposition to the principles of physiological anatomy to assume that the elongated elements of the sieve-tubes simply serve the function of a storage-tissue in which albumen remains at rest until required for use in the immediate vicinity. Frank's process of reasoning will no doubt bring us nearer the truth. According to this authority, the soluble amides and the carbohydrates circulate in the parenchyma. From the amides are formed mucous (undissolved) albuminous substances; in the winter these collect in the sieve-tubes and remain at rest. At the time of cambial activity this mucous mass in the sieve-tube system oscillates, due to the bendings of the stem and changes of the turgor-force accompanied by a gradual reabsorption of the albumen. Frank's studies (and those of his pupils) may perhaps soon lead to the recognition of the fact that the sieve-tubes really form a storage system, but that they are also admirably adapted to permit mass-movement in a longitudinal direction during active assimilation.

Since we have referred to "girdling," we may also mention the well-known experiment which is made as follows: aleaf-bearing twig (of willow) is girdled a little above its leafless, lower end and the cut end placed into moist earth up to a point somewhat above the girdle. No roots, or but very few, appear below the girdle, while numerous roots and callus are formed above it. A current of formative substances passes from the assimilating leaves downward along the cortex; wherever the path is broken, this substance is at once converted into callous tissue.

The movement of undissolved albuminous substances in the sieve-tubes, like that of the milk-sap mentioned above, is a *mass-movement.* The causes for this movement, though not definitely determined, have already been referred to. Gravity, outer mechanical pressure upon the soft elements, and turgor-oscillations in the neighboring tissues no doubt assist in bringing about this movement.

β. Conduction of Carbohydrates.

Here, and in general with substances in solution which must pass through plasmic membranes and cell-membranes, we are concerned with *molecular movements*, which belong to the domain of *osmosis.* General statements only will be made now; particulars will be given below.

The physical considerations of osmotic action differentiate (1) *hydro-diffusion*, the osmotic interchange of two miscible substances without any separating membrane; from (2) *diosmosis* in the usual sense, that is, a process similar to (1) with a dyalizing membrane or porous substance. Both processes occur in the vegetable cell.

Ad 1. In an assimilating palisade-cell exposed to the sunlight several currents must be formed in obedience to the principle that the current is formed at right angles to the lines of equal concentration (see Fig. 60). It is assumed that the maximum concentration of sugar, for example, is at 5 (Fig. 60). The sugar-molecules will then move in the direction of the arrows; the water-molecules in the opposite direction. Wherever a crystal or a starch-grain grows within a cell, there are produced such zones of concentration in the surrounding liquid, and the respective movements will take place.

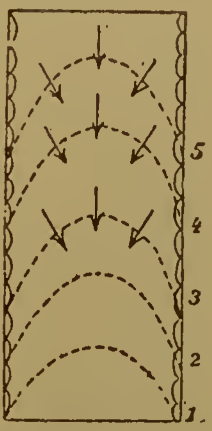

FIG. 60.
(Modified from Haberlandt.)

Ad 2. If the solutions in neighboring cells are of unequal concentration, a new complication arises, which leads us into a branch of physiology, in part, yet unexplained. The more recent investigators (BRÜCKE, PFEFFER) have, however, given many explanations and suggestions. Whatever applies to processes that may be traced to *living* protoplasm is also applicable here; the behavior of the living primordial utricle in the movement of food-substances from cell to cell is not well understood. It is, however, very clear that a living cell in contact with water will increase its hydrostatic pressure by taking in more water.

The so-called *transitory* starch which occurs in the form of small *granules* within the cells in which starch circulates is of special importance in the circulation of soluble starch. We can somewhat understand the function of this transitory starch when we learn that the precipitation of starch-substance in the form of solid granules produces a decrease in the degree of concentration in the surrounding starch solution. As a result new currents are set in motion toward the granules; but why these granules are formed at the suitable moment, and why they are again dissolved in order that the current may continue in the same direction and thus make way for new incoming currents and new precipitates of starch-substance, is but little understood. The processes of hydro-diffusion and diosmosis are, of course, frequently combined in the circulation of food-substances. According to SACHS[1], we may, in general, express ourselves as follows: Every growing part of a plant acts as a centre of attraction for the available food-substances; every storage-tissue or receptacle and every assimilating organ acts as a centre of repulsion as compared with the growing portion.

Many of the earlier and also of the more recent physiological and anatomical investigations, especially those of SACHS, also those of HABERLANDT and of SCHIMPER, throw light upon the conveyance of assimilates from the leaves. We are here concerned principally with the adaptive arrangement of the assimilating cells and other leaf-tissues with regard to the *vascular system* and the mode of conduction within the tissues named (see Physiological Anatomy of the Assimilating System, Function VI). In the early sixties SACHS had already observed that germinating plants free from starch (etiolated) when brought into the sunlight would soon contain small starch-grains, first in the chlorophyll-grains of the leaf, then also in the conducting tissues of the petioles and internodes; these starch-granules would disappear when the plant was placed in the dark and again reappear when brought into the light. As a result of these investigations by SACHS, and also those of more recent authors, we shall here emphasize the fact that the following tissues are especially adapted to conduct starch and other food-substances which are free from nitrogen: the vascular bundle-sheath of the leaf-blade and the parenchyma immediately about the larger bundles, the parenchyma of the petioles and stem-organs, inclusive of the wood-parenchyma and the medullary rays. The "path" broadens continually, similar to the path of blood-circulation in man.

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[1] Vorlesungen, page 439.

γ. *Conduction of Water.*

The history of our science has undergone great oscillations in regard to the movements of water in the plant-body. By "water" we mean the liquids which, as is known, always contain mineral salts and other substances in solution, and which are taken from the soil by the roots.

It is generally agreed that the current of water passes upward in the woody tissue of dicotyledons and conifers, especially in the younger annual rings (splint-wood). Let us further consider circulation in dicotyledons and conifers.

In agreement with many authors, I find it impossible to accept Sachs' theory of "imbibition." The future history of botany will no doubt show that it was the reputation of the originator of this hypothesis that made its acceptance possible for so long a time. According to this hypothesis, we are to assume the following: water does not pass through the cell-cavities (lumina), but through the cell-wall substance. The living woody cell-wall contains water obtained by imbibition, and so long as the cell-wall is not dry this water which has been imbibed is very readily *displaced.* Unlignified (not woody) cell-walls and woody cell-walls which have once become dried do not possess this property. Sachs further emphasizes the fact that the force with which water is retained in the cells which are capable of imbibition is so great that it makes no difference whether the imbibing cell-body lies ten or one hundred metres above the water-absorbing roots, just as in the case of the saline ocean-water it makes no difference whether the salt-molecule in solution floats one hundred or one thousand metres above the bottom of the ocean." If from such a system of water-soaked cells water is removed at one end by evaporation (in the leaves),

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[1] Vorlesungen, page 290.

there is a retrogressive movement of water-molecules induced by this disturbance which continues to the root and which tends to re-establish the "state of saturation."

Critics rightly observe that the great force with which the water obtained by imbibition is held by the molecules of the cell-wall requires a correspondingly great force to separate it from the molecules of the cell-wall and to guide it onward; in other words, the force of friction must be very great. From Schwendener's[1] explanations it is implied that the movement of water in an *imbibing system* is subject to the same law as the movement of water in a capillary system; that therefore the moving force becomes very great as the diameter of the tubes becomes immeasurably small. Schwendener also discusses the differences between capillarity and imbibition as emphasized by Sachs. From this discussion we select the following: Entrance of water into a solid body in the state of aggregation may take place whether the volume of the body remains the same or whether it becomes smaller or larger; in this respect capillarity and imbibition are alike. If we suppose a series of glass plates to be superimposed upon each other, the height of this pillar may be increased if the edges are brought in contact with water, provided the spaces between the plates are not too great. If the intervening spaces are increased above a certain limit, the height of the pillar is reduced by capillary action. Therefore we cannot correctly say that when the spaces of a body into which water enters are pre-formed, and when the limiting walls of these spaces are firm and immovable, friction is great; and if such spaces are not previously formed, but are produced by the water itself, whereby the volume is increased, friction is reduced to a mimimum or zero. There is nothing characteristic of capillarity in the immobility of the walls of a system, therefore nothing essentially different from imbibition accompanied with increase in volume. The term "imbibition" is, however, not superfluous, or synonymous with capillarity. We say a starch-grain is imbibed when it has become saturated with water (from internal causes due to processes of growth (Correns) *without changing its structure.* This condition is strictly different from that of swelling, in which water is also taken up (usually a *greater* or *smaller* quantity than in imbibition, hence an irregular quantity), but from external causes, and always with the result that the structure of the grain is permanently changed. *Imbibed* membranes, as well as starch-grains after drying, can take up a definite amount of water and assume their original volume; *swollen*, similarly treated cell-walls and starch-grains will not assume their original volume (CORRENS). Imbibition is therefore something specific, a taking-up of water without change in structure, a change which can *not* be equally well designated by the term "capillary action."

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[1] Untersuchungen über das Saftsteigen: Sitz.-Ber. der Berl. Akad., 1886.

The ready displacement of water in membranes, mentioned by SACHS,[1] and the great frictional resistance which must exist according to physical laws, are in direct opposition. Moreover, the above-mentioned displacement has not been demonstrated by unimpeachable experiments. *Imbibed* membranes, for example of *Laminaria*, show this high frictional resistance according to the investigations of SACHS. The hypothesis of Sachs had its origin at a time when the anatomical-physiological conception, which later brought about such excellent results, was but little understood. At that time the best workers in our branch of science treated the cell-forms of the plant-body according to a strictly anatomical method based upon the evolutionary history of development so characteristic of NÄGELI and his school. The conclusions of Nägeli and Schwendener's[2] critical speculative studies concerning this subject point to wholly different results and do not formulate a concluded theory. Although these studies preceded the advance made in our knowledge concerning endosmosis, through the investigations of Pfeffer (1877) the conclusions of Nägeli still hold good. They are as follows: "It only remains for us to distribute the water-moving forces among certain numerous points. Since there is no reason why we should concentrate them in definite cells of the tissues, it seems most natural to locate them in each and every cell containing cell-sap. Only when the energies of the tree are equally distributed in all cells are such diminished tensions, as occur in the plant, explainable." SCHWENDENER'S[3] more recent investigations verify his former conclusions as well as those of Nägeli. Based upon these two works (1877 and 1886), and also upon Pfeffer's experiments concerning osmosis, I shall offer the following explanatory statements:

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[1] Porosität des Holzes: Arbeiten des Bot. Inst. in Würzburg II, 1879.

[2] Das Mikroskop, 1877.

[3] Sitz.-Ber. der Berliner Akademie, 1886.

1. Capillarity cannot replace the molecules of water removed by evaporation from the periphery of a tree. In a capillary system one meter in height in which the possible height of the column of water is fifty meters, according to the diameter of the interstices, sinking due to evaporation from a large area is more rapid than the rise due to capillarity. The latter force is therefore without effect for greater heights. This experiment by Nägeli and Schwendener was made with a cylinder of starch-paste in a long glass tube.

The fact that the capillary attraction of the interior of the cell-wall would in itself be sufficient to raise the water-column at least one hundred feet is not of decisive moment, since in a unit of time the sinking of the column due to evaporation is much more rapid than the rising.

2. With reference to water-movements, imbibition of the cell-wall is only a special case of capillary action. In both there is friction of water-molecules upon each other, there is in both a solid framework within which water moves or circulates; firmness and immobility of the enclosing walls are, however, not essential properties of a capillary system. (Compare the above with the statements of SACHS.)

3. The osmotic forces of the *living* cells come into play. Here we must make a distinction between that which osmotic forces can accomplish and that which they can *not* accomplish within the living woody cells, of course only in so far as our knowledge will permit us to see and comprehend. Turgescent living cells no doubt, under certain conditions, will force water into neighboring dead elements (vessels and tracheids) in the same way as they would force water into a vertical glass tube (demonstrated by experiments).

A high hydrostatic pressure within a living cell is produced as follows. The water-attracting force of the substances in solution in the cell-sap (nitrates, sugar, etc.) draws the water which is found in the vicinity of the cell through the cell-wall and primordial utricle into the cell-lumen. The interstices in the living primordial utricle are presumably very minute. As has been demonstrated, the molecules of sugar in solution in the cell-sap require many hours before they will diffuse into the surrounding water. Therefore either the molecules of sugar cannot pass through the primordial utricle, or more molecules of water pass inward than sugar- and salt-molecules pass out. The latter phenomenon makes it evident that such a plasmic interstice has a certain depth and width, but that *water* takes a position at the *periphery* of the same and passes into the cell because of the greater affinity of the saline substance to the water. In the middle of the interstitial canal the salt- and water-molecules move in an equalized or balanced relationship (hydro-diffusion), while in the immediate vicinity of the cell-wall substance there is an excess of water flowing inward. Hence it matters not whether none or a few sugar- or salt-molecules pass outward: water will accumulate in the interior of the cell; the hydrostatic pressure of the cell increases; the cell-membrane, which forms the support of the primordial utricle, becomes more and more tense and in return it exerts an equal pressure, due to its elasticity, upon the cell-contents. It is only necessary to assume that at certain points—doubtless the thin areas of the cell-wall, the pores—the primordial utricle is more readily permeable to water than at other points. If these cells lie in contact with vessels, then the thin areas are comparable to openings at which suction-tubes are placed. If the endosmosis of water in living cells lying near a vascular system continues, the infiltration into the vessels will also continue, and the question arises, How high can the column of water be raised? This height is evidently dependent upon the nature of the primordial utricle, on the composition of the endosmotically acting substances, on the relative concentration and temperature of the liquids, and on the diameter of the vessels. Potassium nitrate, for example, possesses a very high "endosmotic equivalent," as has been demonstrated by PFEFFER. His experiments were made with clay-cells, the interior of which were lined with a film of cupric ferrocyanide. For a one per cent potassium nitrate solution the pressure was sufficient to cause the mercury-column to rise 175.8 cm.

If one supposes the forcing in of water to be interrupted, so that water and air pass into the vessel alternately, there is produced the so-called "chain of Jamin."

Bleeding (Blutungsdruck)—a better term than "root-pressure," because we are not concerned with any specific activity of the roots

—is the term applied to the above-explained process. This phenomenon is referable to living cells in general (experiments with various stems by PITRA and C. KRAUS). Pressure due to bleeding *sinks very materially during the vegetative period.* A safe maximum of this pressure (observed in a grape-vine during the spring) may be represented by a column of mercury about 100 cm. high (HALES). However, as already stated, *the positive pressure is, in general, very materially reduced during the period of maximum transpiration.* If, therefore, the *highest* positive pressure observed can raise a column of water to only 15 m., or usually less—say 2 m.—we cannot rationally explain the rise of the sap by supposing the propelling force to be at the base of the stem (in the root-system) forcing the water upward several hundred feet after the manner of a force-pump. This, however, does not exclude the possibility that osmotic forces of lesser intensity may occur at various heights in a tree and come into active play in the living cells in the neighborhood of vessels and tracheids; in fact, this has been proven in a number of instances. This carries us back to the ideas of Nägeli and Schwendener expressed above.

We must also mention the phenomenon of *water-excretion*, observed in various herbaceous plants by different authors.[1] At night during the spring when the bleeding-pressure is high and transpiration low there are noticeable copious excretions of water at certain areas—for example, from the apices of monocotyledonous leaves as well as from the serrate edges and apices of dicotyledonous leaves. Frequently there exists a special secreting apparatus placed at given points. The water-conducting vessels expand fan-like or brushlike at the points referred to; above the vascular ends there is sometimes a special tissue of colorless cells, the "epithem." Structures resembling stomata (the "water-pores") are found grouped at certain epidermal areas: they facilitate the escape of water.

The above-cited investigations by SCHWENDENER concerning the ascent of sap (1886) give further evidence of progress toward the solution of the problem under consideration, although we are far from a satisfactory explanation. Among others the author[1] has carried on some special investigations in regard to this problem. I wish to state in advance that Schwendener for a time withheld judgment in regard to my conclusions, but that he defended some of my propositions against attacks. Therefore before entering more particularly into Schwendener's important investigations I will here introduce my explanation.

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[1] SACHS, Experimental Physiologie (1865), p. 236. Also more recently VOLKENS, Über Wasserausscheidung, etc., Dissertation, Berlin, 1882.

According to my interpretation, there are two forces employed in the ascent of the cell-sap: 1, endosmosis; 2, capillarity—the former a moving force, the latter a holding or retaining force. Two forms of elements represent the path in which cell-sap moves; namely, living cells, the wood-parenchyma and the medullary rays in particular; also the dead elements, vessels and tracheids. Endosmosis acts as a propelling force in a twofold way: by *forcing water* into the dead elements at one point, while at some more elevated point the living cells take up the same and *conduct it for a short distance from cell to cell by endosmotic suction.* This proceeds in a longitudinal direction to a point bearing less water, hence upward, where it will again be forced into the tracheal system. Capillarity simply acts as a *retaining force,* since the columns of water are self-supporting.[2] In the remaining explanations I will utilize the accompanying diagramatic figure, in which *A*, *B*, *C*, and *D* represent different elevations in the stem, *G* a vessel, *m* the medullary rays, *hp* the woody paren-

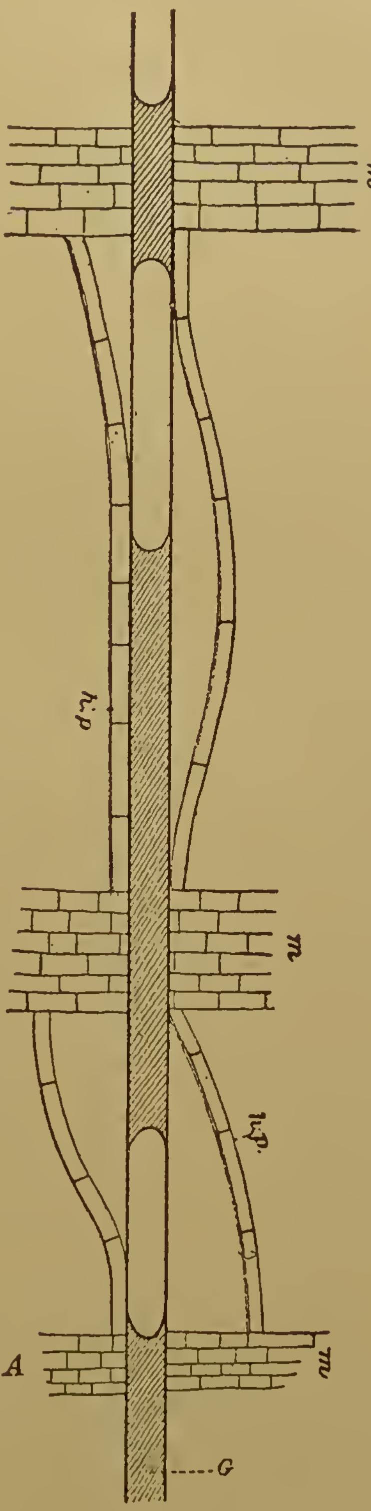

Fig. 61.

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[1] Berichte der Deutschen Botanischen Gesellschaft, 1883, and Sitz.-Ber. der Berl. Akad., 1884.

[2] Zimmermann's investigations in d. Ber. der Deutsch. Bot. Ges., 1883.

chyma. The water-reservoir of the root-system extends its influence up to the medullary rays at the levels *A*. It is only necessary that endosmosis (suction) should act from cell to cell through the parenchyma until the medullary-ray system *B* is reached; here the water is forced into the vessel until it rises to *C*. From there on endosmosis again acts within the parenchyma as far as the medullary ray in *D*. The periodic oscillations in the bleeding-pressure observed by various investigators are worthy of note. We may assume also that in reference to bleeding a minimum, optimum, and maximum temperature has some influence on this process.[1]

From Schwendener's communication on the ascent of cell-sap the following important statements are selected. 1. Every local suction or pressure continues to act only in those particles of wood in which there are connecting water-threads or columns. 2. Breaking of the water-columns or threads by air-bubbles produces a high degree of immobility within the vessels. Air-bubbles in an isolated vascular tube act differently from those in a tracheal system. The Jamin's chain already referred to is formed in the vascular tube. During the summer the bleeding-pressure in the stem of a tree will allow only the escape of sap without any air-bubbles, even when vessels and tracheids (libriform) are richly supplied with air. This water (without air-bubbles) comes from the tracheids, and not from the *vessels*. The resistance in the Jamin-chain within the vessels is too great to allow bleeding-pressure to set the entire chain in motion. However, the mass of water can move onward through the pores of the cell-walls by the completion of the water-column through laterally uniting water-columns and threads in the system of tracheids, while the enclosed air-bubbles *remain stationary*. As a rule, the air-bubbles are in the middle of the tracheids.

The ready displacement of water within woody tissues sufficiently supplied with water depends *upon the presence of continuous water-threads*. Placing a drop of water upon a cross-section of green wood several metres in length at once causes the escape of a drop from the other end ("HARTIG's experiment").

A few words shall be added concerning the effect of rarefied air, in other words concerning the physical process of suction (endosmosis) within the wood.

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[1] See PFEFFER's Pflanzenphysiologie.

It might have been stated above that high *negative* pressures have not been observed in the tracheal system at a considerable height (of a tree); neither have high positive pressures been observed in the lower part of a tree-trunk. This evidently tends to prove that capillarity is not the *moving* force. It is certain, however, that spaces containing rarefied air do occur in the vessels or in the tracheal system. The question that arises is, What can endosmosis, as the result of rarefying air, accomplish in the tracheal system by way of elevating water? In regard to this question many authors hold erroneous opinions. SCHWENDENER, ZIMMERMANN,[1] and GODLEWSKI[2] have opposed these opinions. I will here only add from the recent work of Schwendener[3] that the lifting power due to suction, assuming the water-columns to be 10 mm. long and the air-columns to be of equal length, may be from 13 to 15 m. However, the water-columns observed in trees *after* the time of "bleeding" were much less than 10 mm.

We are approaching the close of this subject, and shall now state that which at present seems to be the authoritative final explanation of the water-movement in plants: dead elements are essentially the paths in which water moves, while the living cells supply the propelling force for the transpiratory current of water.

Experiments which show that water movements in a living tree will also continue through dead segments (killed by steaming, poisoning, etc.) do not prove that living cells are unnecessary to the ascent of sap (Schwendener); such dead portions presumably contain more than the usual quantity of water in the tracheal system at the beginning of the experiment, later, very likely, Jamin-chains.

The following is additional evidence of the correctness of the foregoing fundamental ideas: the contact and relation of communication between the dead tracheal system and the system of living cells in the vascular bundles and plant-organs; the occlusion of vessel-lumina by means of tyloses and callus in the case of injuries; and the reduction or almost entire absence of vessels in submerged water-plants whose needs for a water-conducting system are very small or nearly, zero. The special anatomical structure of vascular walls, namely their ability to withstand the high radial pressure which proceeds from turgescent cells, can only strengthen our conclusions. FRANK[1] calls attention to the fact that the large amount of water required to supply the numerous leaves in the spring coincides with an adaptive development of numerous large vessels and tracheids.

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[1] Ber. der Deutsch. Bot. Gesellschaft I, 1883.

[2] Pringsheim's Jahrbücher XV, 1884.

[3] Zur Kritik der neuesten Untersuchungen über das Saftsteigen, Sitzungsber. der Berl. Akad., 1892.

PROTECTIVE SHEATH OR ENDODERM.

(CONCLUDING CHAPTER TO THE THREE FOREGOING ONES ON SPECIAL FUNCTIONS.)

CASPARY'S term *protective sheath* as well as the term *endoderm* proposed by DE BARY are equally correct designations for the tissue-system under consideration. *Normally this structure occurs in the roots;* it is also found frequently in stem-organs, even in the leaves. Its functions are: 1. Mechanical; the delicate elements of the leptome (albumen-conducting tissues) must be protected against injuries; the endoderm encloses these delicate tissues in the form of a hollow or fluted cylinder. 2. In case of the loss of the peripheral *root-parenchyma* and the *root-epidermis* it functions in their stead by forming a protection against evaporation as well as a protective tegumentary covering. 3. In case the root remains intact it restricts the interchange of cell-sap in the vascular bundle by its relative impermeability to water-solutions. 2 and 3 may be looked upon as those functions which would make the term "endoderm" (inner tegument) especially applicable.

The following statements will explain the nature of mechanical injuries against which the endoderm forms a protection: Delicate sieve-tube tissues are subject to torsions and stretchings due to changes in turgor-pressure within the contiguous succulent parenchymatous tissue. If these lateral and longitudinal tensions proceeding from the parenchyma are to be harmless to the delicate sieve-tube tissue, they must be enclosed by tissue-elements which will neutralize or counteract these tensions. Thickening of the cell-walls of the endoderm serves to supply the mechanical requisites; in extreme cases the "simple" protective sheath receives a number of thick-walled supporting layers. *Suberized walls without thickening* very frequently assist the mechanical function. In the first place it is a mistake to suppose that completely suberized cell-walls are in general very extensible; the thin-walled corky layer of birch-bark proves the contrary. (Actual tests in regard to the elasticity of suberized protective sheath-cells are wanting.) In the second place we may ascribe considerable absolute firmness to the suberized cell-walls. (Based upon actual observation.)

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[1] Lehrbuch der Botanik, Leipzig, 1892–1893.

The relative impermeability of suberized cell-walls to water-solutions and water-vapors is known from what has already been stated.

It will not be difficult to illustrate what has been said of these anatomical relations by studying a dicotyledonous and a monocotyledonous root. In passing, it may be recalled that the above mechanical function is immediately related to the utilization of thick-walled cells for the purpose of "local protection," as was mentioned in the discussion of the mechanical septum.

The root of *Allium ascalonicum* (monocotyledon) (Fig. 62) shows the protective sheath between the parenchyma and pericambium. The *thick*-walled and the *thin*-walled cells of the protective

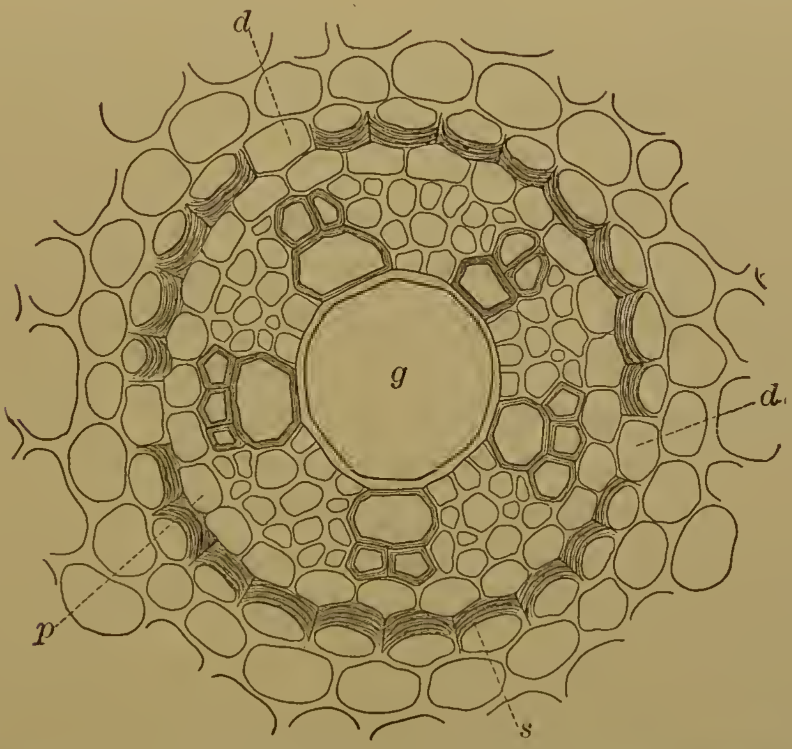

Fig. 62.—Central vascular system of the root of *Allium ascalonicum*.

g, Large vessel; *s*, bundle-sheath with passage-cells (transit-cells), *d*; *p*, pericambium. (After Haberlandt.)

sheath, that is, the characteristic thickening of the cell-walls next to the leptome, and the thin-walled cells (passage-cells or transit-cells) which form the "channels" of communication that is, points of interchange of liquids (cell-sap, etc.), between the parenchyma and vessels. *Vicia* root (Fig. 58) shows the frequent, but not readily understood, formation of the protective sheath as it usually occurs in dicotyledonous roots and in the stems of water-plants. The thin-walled cells of the protective sheath are here either *partially* or *totally* suberized; in the former case only the radial walls or sometimes only the middle portions or bands of the radial walls; even with such partial suberization the bands form a continuous hollow cylindrical network. In its mechanical function this cylindrical network may be compared to the protective net-work of rope enclosing a balloon (SCHWENDENER). In the case of the vascular bundle of the root the pulling tensions are of course on the outside, and not on the inside, as in the balloon. The following will serve to explain the dark spot ("Caspary's dot") seen on the radial walls in cross-section (Fig. 58). They are local thickenings of the cell-walls (Caspary). The suberized bands of the cell-wall are only slightly extensible, and hence only slightly contractile. The unsuberized walls of the neighboring cells and the unsuberized portions of the sheath-cells are highly elastic and become expanded by the turgor-force, but contract again as soon as turgor is suspended; the less elastic portions can only adapt themselves to this contraction by forming wavy foldings (Schwendener). These wavy foldings can be seen in tangential sections. The dark spot seen in the cross-section is only the optical effect due to the membranous folding. When the tangential walls are unsuberized, the above-mentioned "limiting" or "bounding" function is excluded (see 3, page 118).

Roots of ferns growing upon walls and rocks, and hence exposed to great variations in the supply of water, have enormously developed protective sheaths. (For particulars see SCHWENDENER's communication on Protective Sheaths and their Strengthenings.)[1]

Without in any way interfering with subsequent statements, we shall here briefly consider SCHWENDENER's[2] more recent investigations on the mestome-sheaths of gramineous leaves. The phytotomist in the study of the leaf anatomy frequently observes that the vascular bundles, especially of the monocotyledons, are supplied with a thickened endoderm (*mestome-sheath*), and in addition, immediately outside of the same, a "parenchymatous sheath," which is usually chlorophyll-bearing and which we have already referred to in the discussion of the conducting system. As examples in which this occurs we may mention *Poa pratensis* and *Bambusa vulgaris.* In the absence of the mestome-sheath it frequently happens that the parenchyma-sheath, although belonging to the conducting system, shows modifications in its structure (thickening of walls, suberization, etc.) which enable it to perform the function of the endoderm. *Vice versa* it may happen that in the absence of the endoderm a part of the mestome-cells, especially a crescent-shaped group of the leptsome-parenchyma, may become thickened and so perform a mechanical function.

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[1] Die Schutzscheiden und ihre Verstärkungen: Abhandlungen der Berliner Akademie, 1882.

[2] Sitzungsber. der Berl. Akad. 1890.

V. PROTECTION OF THE MERISTEMATIC AREAS OF THE PLANT-BODY.

Young, undeveloped leaves perform a service for the apical area of the stem similar to that which the root-cap performs for the root-apex. The rolling-in of the young leaves of ferns serves a purpose similar to that which sinking-in of the apical area does in the algæ (*Fucus*, *Laurencia*). The leaf-sheaths of grasses and *Equisetæ*, and the sheath enclosing the growing peduncle of *Armeria*, serve a similar function for the internodes which they enclose as does the collenchyma in firm growing tissues. With these statements we have hastily sketched the teleological significance of the subject under discussion. In all cases we are concerned with the protection of delicate meristematic tissues against definite mechanical injuries as well as against injuries in general.

The special consideration of individual cases will give us an opportunity to mention important facts pertaining to the development of the leaf.

(*a*) *The Protection for Terminal Meristematic Areas of the Plant-body.*

α. *Protection of the Root-tip.*

The growing root-tip forcing its way between particles of soil is supplied with a specific *protective organ*, namely, a bell-shaped tissue generated from the interior, but the history of its growth and development may differ very much in different cases. Behind the *root-cap*, as this organ is called, lies the true *root-body*, which is especially adapted by the numerous root-hairs on the outer surface to take up food-substances. The root-cap therefore covers the cell-forming vegetative area, which could not withstand the friction caused by contact with the sharp-angled particles of earth.

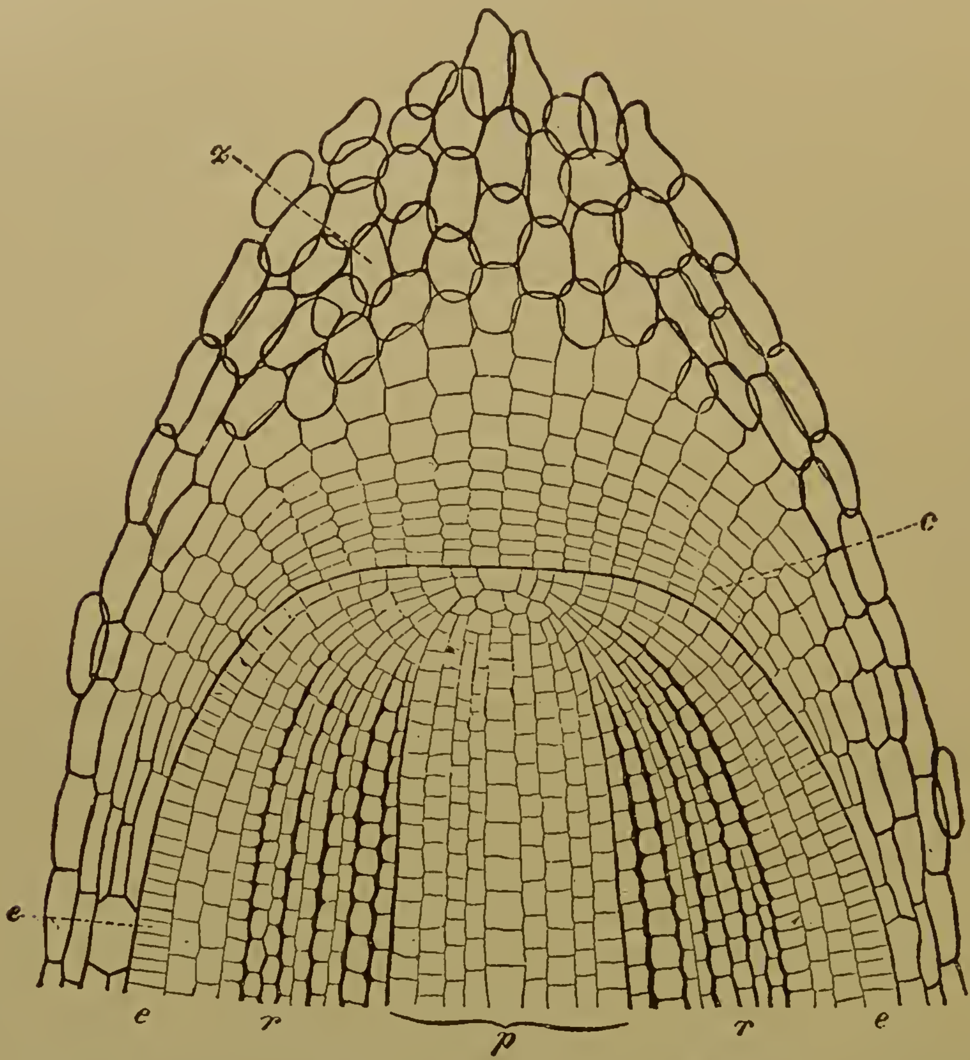

FIG. 63.—Longitudinal section of the root-tip of *Eriophorum vaginatum.* *z*, *c*, Root-cap; *e*, epidermis; *r*, parenchyma; *p*, vascular system. (After Haberlandt.)

The root-cap may 1. develop from a formative tissue designed for that purpose; examples: *Triticum repens* (α), *Calla palustris* (β.) In type (α) there is a sharp distinction between the meristem of the root and that of the root-cap; in type (β) there is no such distinction.

2. These two types among monocotyledons are represented by two corresponding types among dicotyledons, but which differ es-

sentially in that it is the epidermis of the root from which the root-cap is developed by centripetal cell-division and branching. In this case the tissue which forms the root-cap bears root-hairs at some distance behind the tip of the root. If we designate the tissue which forms the root-cap of dicotyledons as *calyptrogen*, that of monocotyledons should be called "dermocalyptrogen." The *Helianthus* or *Brassica* type corresponds to 1 α, that of *Pisum* to 1 β.

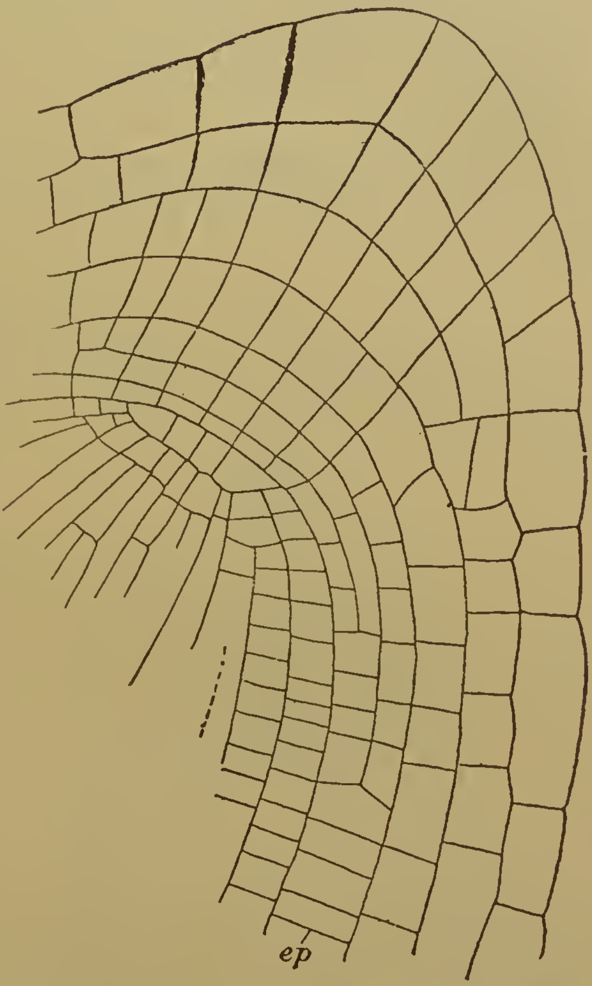

FIG. 64.—Root-tip of *Lepidium sativum*. *ep*, Epidermis. (After Schwendener.)

3. The *parenchyma*, either the outer layers or the entire tissue, may form the root-cap by the branching of the cell-layers, as in the gymnosperms *Juglans regia* and *Cæsalpinia brasiliensis*.

4. The *apical cell* (event-

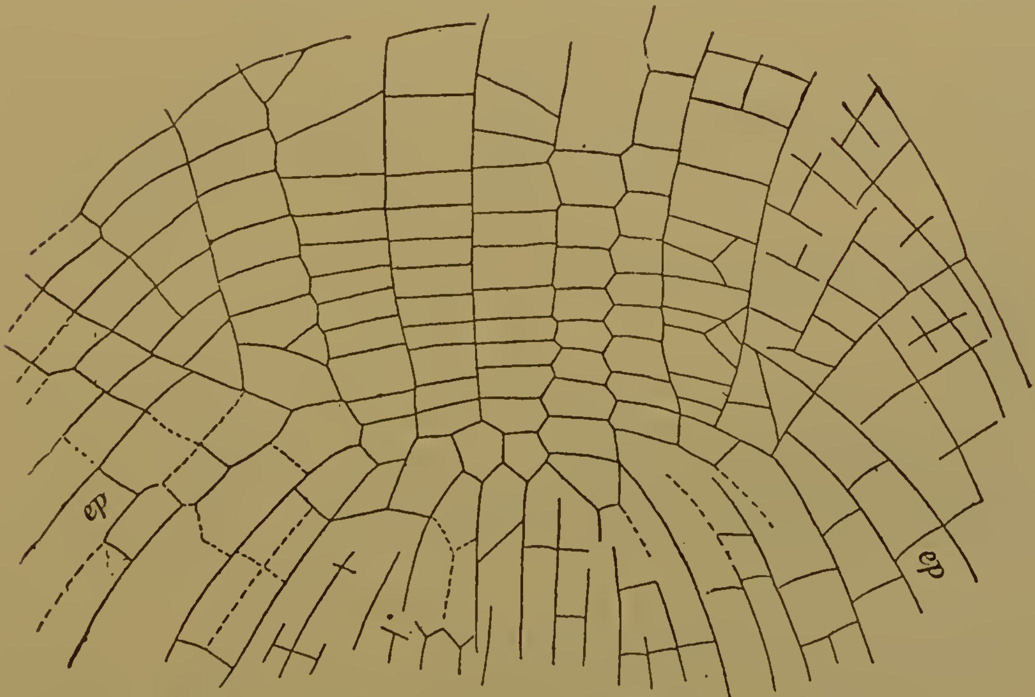

FIG. 65.—From the root-tip of *Cytisus racemosus*. *ep*, Epidermis. (After Schwendener.)

ually the four apical cells arranged in a quadrant) forms cells ("segments") toward the side of the root; occasionally also cells ("root-cap segments") which form the root-cap: ferns and *Equisetum*.

Fig. 63 represents type 1 α, Fig. 64 type 2 α, Fig. 65 type 2 β. The fern type is represented in Fig. 29, p. 47.

β. *The Protection of the Stem-apex.*

1. Normally the apical area of the stem has no *specific* organ which serves as a protective covering for its vegetative area, although it is evidently in need of one; such protection is supplied by *the young leaf-bud, which forms a covering of many layers.* Fig. 66 *a* illustrates this condition. Numerous examples of this kind may be observed in longitudinal sections of leaf-buds, bulbs, etc. Fig. 66 *b* is intended to represent in general a longitudinal section of a stem with *blunt* apical area. Besides these most common forms of protection, there are a few others, namely:

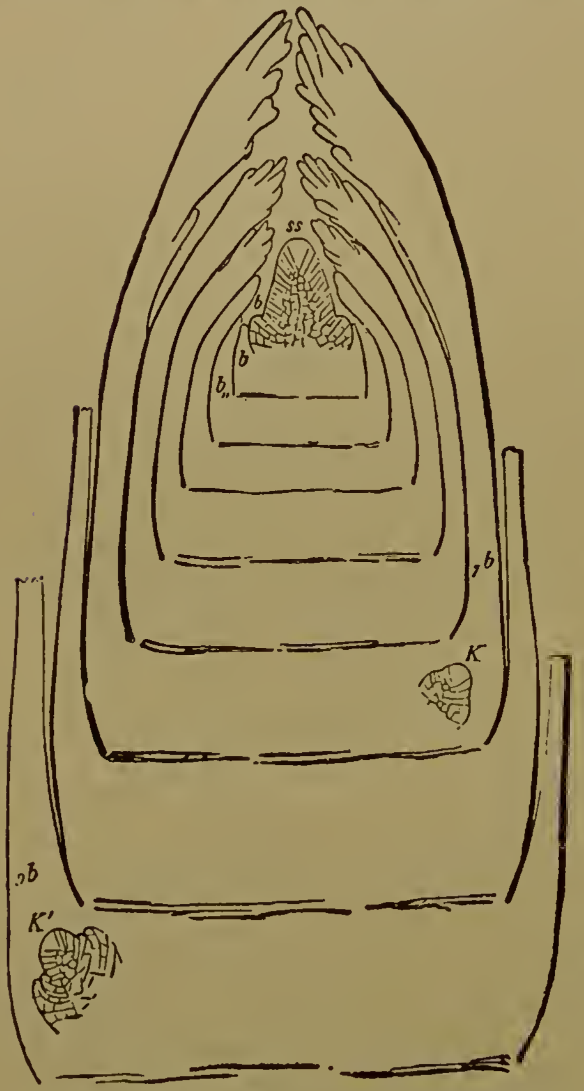

Fig. 66 *a*.—*Equisetum arvense.*
Longitudinal section of a subterranean bud with apical cell (*ss*), young leaves (*b*), and two lateral buds (*KK'*). (After Sachs.)

2. The depression of the apical area; example, algæ, in which the *apical cell* lies at the bottom of a hollow or depression (*Fucaceæ*); we may also mention inferior ovaries (cup-shaped receptacle or torus). From a physiological standpoint we must also include the morphological rule that normal lateral buds appear *axillary*, that is, in the axis of a leaf.

3. Protection by means of *rolling in* is shown in *Florideæ* (red marine algæ).

γ. *Protection of the Leaf-tip.*

The following is immediately associated with what has just been stated (3). An interesting and at the same time easily demonstrable means for the protection of growing organs is to be found in *leaves* of ferns. The leaves of the ferns are an exception to those of numberless other plants in their mode of development (Wedel). Most leaves (phanerogams) develop so that the tip or apex ceases to grow first, the base last. In this and in the overlapping of the leaves in the bud lies the protection for the meristematic portions of these organs. Fern-leaves, however, are peculiar in having a long-continued *apical* growth from an apical cell: the tip therefore requires some form of protection for a considerable period of time; this is supplied by the well-known *spiral* (circinate) *rolling* of the leaf-tips.

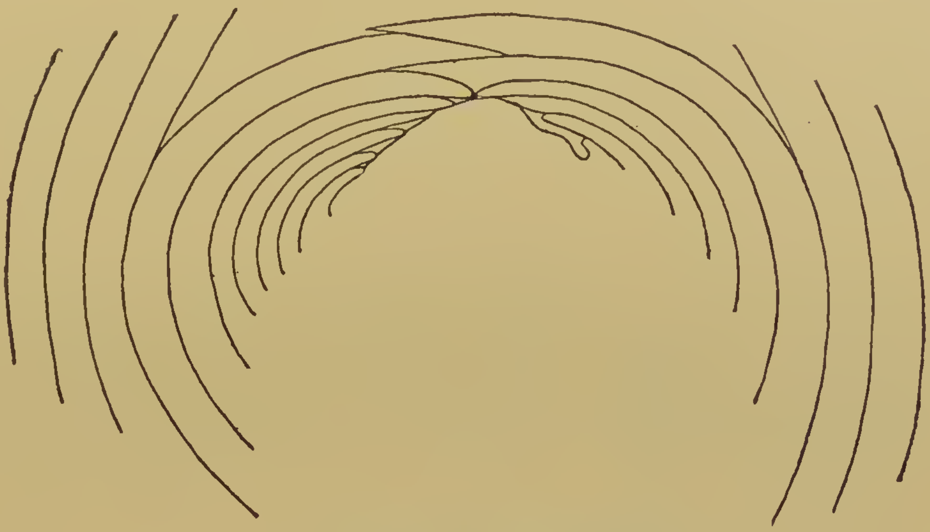

FIG. 66 *b*.—(Diagramatic.)

(*b*) *Protection for Areas of Intercalary Growth.*

In this category of protective adaptations we are in part concerned with evident *mechanical* relations. Accordingly at least a part of this discussion might have found a place in the treatment of the mechanical tissue-system. I believe, however, that it may well be introduced at this point. In the first instance we are concerned with firm organs, stems in particular, which become elongated at interpolated zones ("intercalation"). It is evident that these growing zones consist of delicate and yielding tissues; therefore they represent the weakest points in the mechanical structure of the stem. At these points bending or breaking, due to lateral forces, would most readily take place. The adaptations which occur in the plant creation to protect this process of growth by intercalation were also revealed by SCHWENDENER's investigations, concluded in 1874.

There are two essential means for securing this protection. In the one case it is the employment of a special tissue-system with specific physiological properties. As is known, typical mechanical cells are either lifeless or at least incapable of elongating after they have once acquired their extensive wall-thickenings; they can therefore not exist in growing organs. This special mechanical tissue is the *collenchyma*, which we learned to know in the chapter on the cell. It is very readily recognized by the characteristic thickenings of the angles of the cell-wall. In spite of these thickenings it is *capable of growth.* This tissue has approximately the same firmness (extensibility) as the typical mechanical tissue, but is peculiar in that it becomes permanently elongated (without tearing) when subjected to a slight pulling force (AMBRONN). Collenchyma frequently serves to *strengthen the growing* internodes of dicotyledonous stems (*Compositæ*, *Umbelliferæ*, *Labiateæ*, etc.). This arrangement may in many cases be combined with the second form of protective adaptation, which we shall now consider.

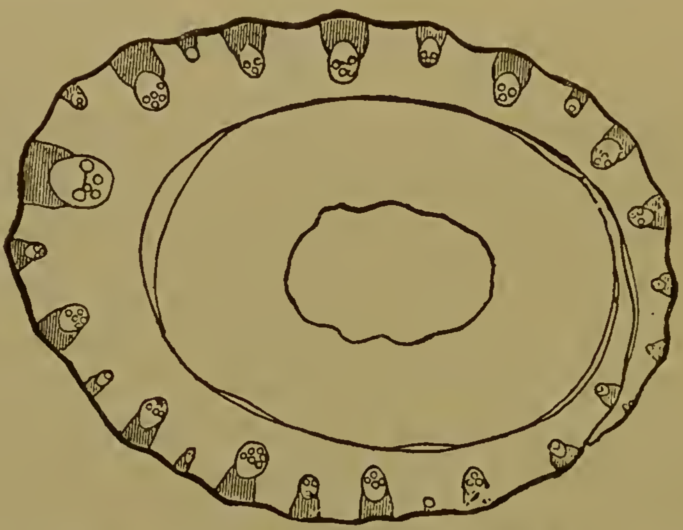

FIG. 67.—Cross-section of the leaf-sheath of *Brachypodium silvaticum*. (After Haberlandt.)

The envelopment of the growing stem by supporting tubes is of very frequent occurrence among monocotyledons, less frequent among dicotyledons. The leaf-sheaths of *Gramineæ*, *Cyperaceæ*, and of *Equisetæ* perform this function by enclosing the growing (as a rule the basal) portion of the internode from which the node projects after it has become sufficiently strengthened. The nodes of grass-stems, and also the region above, are interesting structures for investigation and study; some of their peculiarities, especially geotropic curvatures, will be discussed later. Fig. 67 and 68 will aid in explaining what has just been said and that which is to follow.

In Fig. 68 the *typical* mechanical tissue which has lost the power of growth is colored black. The supporting tube (leaf-sheath) *s* encloses the yet *weak* and *cambial* base of the stem *h*; *s* extends above the cambial portion of the internode. At *co* the mechanical tissue-system is not composed of typical bast but of *collenchyma*, therefore *capable of growth*. If a grass-stem is placed in a horizontal position, the more rapid growth of the lower side of this collenchymatous node will cause it to rise to a vertical position. The firm and more mature portion of the stem within *co* is thereby passively bent.

A rare case, occurring so far as known only in the genus *Armeria*,[1] has been observed and may be briefly mentioned. The mechanical sheath of bracts at the base of the inflorescence extends from above downward; the growing part of the peduncle lies at the upper end of the internode. The sheath is completely formed in the young plant, and after the peduncle has completed its growth it dries up and finally becomes torn.

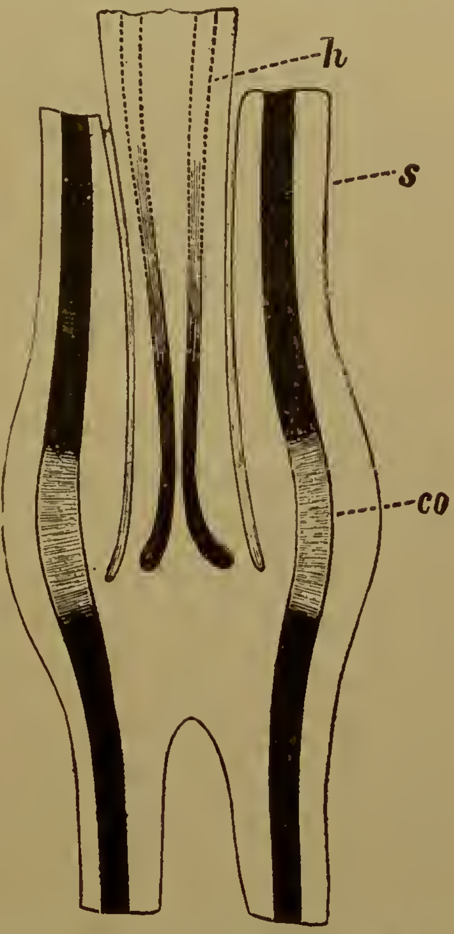

FIG. 68.—Longitudinal section through the node of a grass-stem.
(Diagramatic after Schwendener.)

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[1] Reported by the author in 1881 (Monatsber. der Berl. Akad.). Professor *Schwendener*, who has done so much for scientific teleology, during one of his excursions in the vicinity of Berlin, expressed an opinion, as to what was probably the true state of the case, which led me to make more exact investigations.

A third means of protecting areas of intercalary growth may be mentioned, namely, the *increase in diameter* in the region of the growing zone. *Tradescantia erecta*, according to Schwendener, is one of those plants in which basal growth of the internode takes place; it has internodes in the form of truncate cones. Exact measurements in regard to the course of intercalary growth have not yet been made.

With reference to the *intercalary* (*basal*) *growing leaves*, which include the great majority of leaves, it may be stated briefly that the growing areas are protected by the enveloping sheath-like leaf-blades (elongated monocotyledonous leaves) as well as the overlapping of the leaves in the bud (dicotyledonous leaves).

Among conifers there are membranous sheaths consisting of the bud-scales which enclose the leaf-base.

VI. FOOD-SUBSTANCES DERIVED FROM THE ATMOSPHERE. ASSIMILATION OF CARBON IN GREEN ORGANS.

The dry (solid) substance of the plant-body is, for the most part, the transformation product of atmospheric carbonic acid (CO_2, carbon dioxide). Pure carbon (C) constitutes about one-half of this dry substance, and is found in chemical union in the cellulose of membranes, in starch-grains, in fats, in plasm, etc. C appears in the green organs as gaseous CO_2. CO_2 unites with the elements of water (H_2O) through the influence of sunlight on chlorophyll, forming starch or some allied compound and setting free oxygen (O). These transformations take place in a very short period of time. The greater part of the plant-body (plasm and cell-walls) is therefore derived from the atmosphere.

That carbon dioxide and water form the starting-points for the production of starch as well as for other related substances, with liberation of O, is well known; also that these transformations may take place in a few hours or minutes. But the most discerning chemists at present refrain from attempting to explain the individual chemical reactions involved in the important processes of assimilation. In general, the following formula may be considered as correct: $12CO_2 + 10H_2O = C_{12}H_{20}O_{10}$ (starch) $+ O_{24}$; while the gas-volumes remain nearly the same.

The most important bearers of the assimilating function are the *chlorophyll-bodies*, which have a discoid form, among algæ a band-like, flattened or stellate structure. A definite tissue in which they may occur is not always necessary, though we usually speak of assimilating *cells*, forming a specific *assimilating tissue* which is found in the true assimilating organs, the green leaves. The principles which underlie and regulate the function of chlorophyll-bodies, that is, the conditions under which they can perform their most favorable activity, also underlie the structure of the tissues and the organs which serve the function of assimilation. We will therefore next consider the structure of the assimilating tissue-system.

(*a*) *The Structural Principles of the Assimilating System.*

G. Haberlandt and Stahl have within more recent times made important investigations in regard to the physiological anatomy of assimilation; to these, among others, must be added the communications of Heinricher. From a *physiological* standpoint the communications of Sachs are the most important.

The Greatest Possible Utilization of the Luminous Effects of Sunlight by the Chlorophyll.—Following in thought the problem suggested by this statement leads us to the essential points of view which give us a physiological understanding of the structure of the assimilating organs. When I say "greatest possible" utilization of sunlight, I wish to explain, in order to avoid erroneous conceptions, that the nature of chlorophyll is such that assimilation reaches its optimum with *certain light-intensities;* beyond these an injurious influence makes itself felt. Similarly with the amount of CO_2 present: increasing it to 8 per cent with high intensity of light there is still noticeable an increase in assimilation. Physiology must here likewise be satisfied with a causal-final or teleological explanation of the anatomical adaptations; a causal-mechanical explanation is impossible.

The principle of the *surface expansion* of the leaf which manifests itself by the outer form is still more evident in its anatomical structure (Figs. 69, 70, 71). A maximum expansion of cell-surface is obtained by membrane-foldings, by the regular form and large numbers of assimilating cells. Such adaptive arrangements make room for the numerous chlorophyll-grains which are always adjacent to the cell-wall. The regular, elongated *palisade*-cells with their extensive cell-wall areas, the "arm-palisade" with its foldings (or incomplete cell-walls), are also formed on the principle of great surface expansion. It is of course necessary that these cell-wall surfaces occur on the side of the leaf exposed to sunlight.

The arrangement of these walls and their foldings are also to be considered in their relation to other requirements; first of all they serve to *conduct the products of assimilation* by the *shortest route possible*, and at the same time permit light to pass to the more deeply seated cell-layers. There is, no doubt, a reciprocal relationship between the light-intensity and the perfection of the assimilatory tissue-system, in that the constant lateral position of the chlorophyll-bodies in the palisade-cells (movement of the chlorophyll-grains within the palisade-cells is only an exceptional phenomenon) is most suitable for strong light-intensities (Stahl). However, the structural conformation to strong light-intensities does not take a higher rank than that for conveying food-substances by the shortest route possible (Haberlandt). That the latter is indeed a principle of prime importance can be seen by glancing at the figure of *Silphium laciniatum* (72); further, also, from the fact that there is a group of plants in which the assimilating cells are at the same time conducting cells; they extend parallel to the leaf-surface, either in a direction toward the leaf-base or toward the median vein (leafy mosses, some monocotyledons).

In the case of *Silphium* (see Fig. 72) we can see that the positions of the cell-wall bounding the intercellular spaces (*i*), although eventually exposed to strong illumination, are lined with chlorophyll-grains, while the portions of the cell-wall which cross the current of assimilates at right angles are free from them: this is an example of the predominance of the principle of conduction.

Finally, there are cases in which the palisade-cells are *radiately arranged* about a vascular bundle, which unmistakably indicates that the principle of conduction by the shortest route possible is of prime importance. The palisade-cell placed at right angles to the leaf-surface is only a very frequent special case in the series of elongated assimilating cells.

With reference to these adaptive relations we shall, with Haberlandt, place the arrangement and position of the palisade-cells under the principle of conduction by the shortest path. Stahl is inclined to consider the adaptation to light-intensities as the most

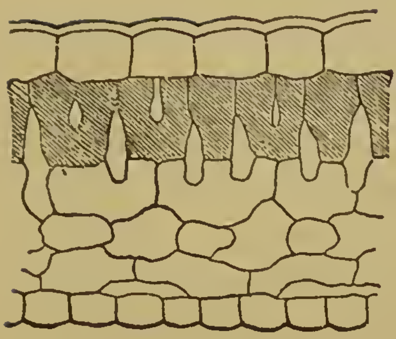

FIG. 69 *A*.—Vertical section through the leaf of *Sambucus nigra*. "Arm-palisades."
(After Haberlandt.)

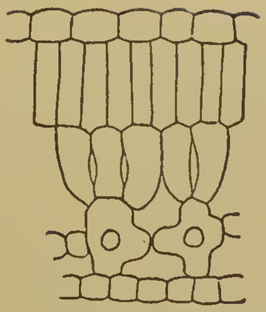

FIG. 71.—Vertical section through the leaf of *Juglans regia*.

Palisade-cells are supposed to be richly, the spongy tissue cells less richly, supplied with chlorophyll. Both cell-forms are here typically developed. (After Haberlandt.)

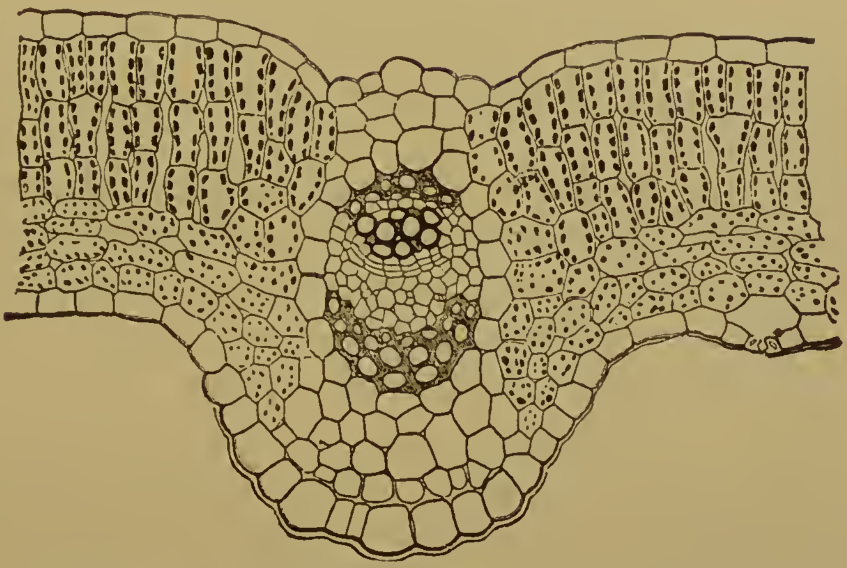

FIG. 69 *B*.—Vertical section through the leaf, including the midrib, of *Raphanus sativus*.
(After Haberlandt.)

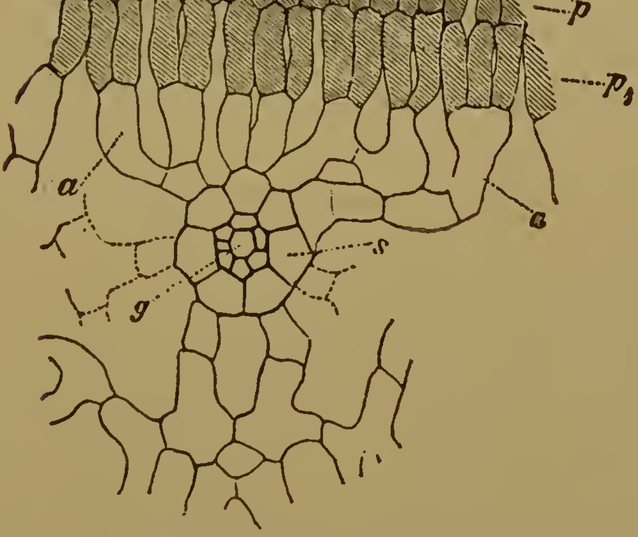

FIG. 70.—Vertical section through the leaf of *Ficus elastica*. The epidermis is omitted.

p and p_1, Palisade-cells ; *a*, collecting cells ; *s*, parenchyma-sheath ; *g*, vascular bundle. (After Haberlandt.)

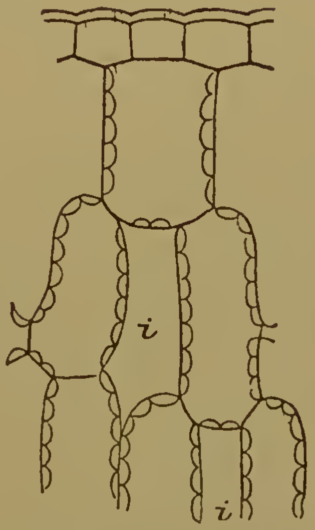

FIG. 72.—Lower surface of an "isolateral" leaf, *Silphium laciniatum*.
(After Haberlandt.)

important. Nor do we deny the correlation of the adaptations. The arrangements of the palisade-cells at right angles to the leaf-surface is the most common position of assimilating cells, because here illumination is as a rule most perfect or intense; furthermore, the adaptive development of *one* side favorable to light in leaves illumined on one side, and the adaptive development of *two* sides favorable to light in leaves illumined on both sides (isolateral leaves), are additional evidence of this correlation, and, in general, the correlative arrangement of typical assimilating cells. Finally, light-intensity and anatomical structure give expression to this correlation in the differences of sun-leaves and shade-leaves which develop on the same plant or plant species. The difference is particularly noticeable in the *stronger* development of the palisade-tissue in the sun-leaf (Stahl).

In addition to the two structural principles of Haberlandt—surface expansion and shortest path for the assimilates—we may add a third structural principle harmonizing with existing facts, namely, Stahl's principle of the adaptation to light-intensity. From the above arguments we must consider this relation to light as a structural principle belonging to this chapter. In one respect these three principles are very much alike: all are readily understood from a teleological standpoint, not one is explained casual mechanically. The factor light *must* invariably be brought into consideration.

Below the palisade-cells of the luminous side of an ordinary horizontal leaf lies the loose *spongy tissue*, so named, because of the large intercellular spaces and irregular cell-forms. This structure, which is also shown in the accompanying figures, is characteristic of the lower surface of the leaf. It evidently serves to perform several functions: (*a*) the conveying of the products of assimilation to the parenchyma-sheaths of the vascular bundles; when the processes of differentiation have progressed somewhat more, we may also distinguish "collecting cells" (see Fig. 70, *a*); (*b*) an assimilating activity because of the chlorophyll present. We must also bear in mind the self-evident result of the bounding of numerous cells by intercellular air-spaces, that is, considerable transpiration must take place. The author, however, agrees with Volkens who looks upon this transpiration as a process physically necessary and which produces physiological effects, but which in itself is not a physiological function. We must, however, ascribe to the spongy tissue a *third essential* function, namely, the *aeration* of the typical assimilating tissue (the palisades). The latter contains numerous but narrow air-channels which are arranged about each palisade-cell; but the supply of CO_2 and the nearest centres of accumulation for the liberated O are naturally to be sought for in the spongy tissue, since it communicates directly with the *atmosphere.* Particulars will be given below (VII., Special Function).

The teleological consideration of nature suggests that not all leaves met with in nature are built "bifacially" and equipped with anatomically different light- and shade-surfaces. Observation teaches that beside the large number of flat leaves placed horizontally there are many of cylindrical form (linear leaves), and others which are flat, but not horizontal, either having the margin turned toward the stem (*Callistemon*, *Lactuca scariola*) or placed approximately vertical. The latter position occurs among some grasses, among orchids, in *Acorus*, etc. From this may be deduced the following:[1]

A. A "centric" type of structure with a *two-sided* or cylindrical evenly developed chlorophyll-bearing parenchyma is peculiar to those flat leaves not horizontally placed, as many grasses, orchids, *Acorus*, *Lactuca scariola*, *Callistemon*, etc. (see Fig. 72). Also those leaves approximately cylindrical—needles, so called. To the latter should also be added the green culm-like stems (*halmartige Stengel*).

B. The majority of leaves belong to the bifacial type and are always flat and placed horizontally. I shall not hesitate in citing a very striking example of adaptive phenomenon. The leaves of *Allium ursinum*, *Alstrœmeria*, and others, in their early development cause the morphologically lower surface of the leaf to be turned upward by a torsion of 180° of the petiole or leaf-basis. *In these leaves* the morphologically lower surface possesses the structural arrangements for active assimilation. An analogous example has been observed by SCHWENDENER in the mechanical adaptation of the leaf of *Gynerium argenteum.*

The same physiological significance as that of the mormal bifacial leaf-structure also underlies the fact that in the lichens the assimilating algal cells ("gonidia") are found nearest the luminous side of the leaf-like thallus (see the chapter on symbiosis).

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[1] DE BARY, Comparative Anatomy, page 406, *et seq.*

The physiology of the phenomena of movements will acquaint us with adaptive movements which will bring the leaves into the most suitable positions with reference to the sunlight. The chlorophyll-bodies themselves have special adaptations for the maximum utilization of the sun's rays.

(*b*) *Movements and Changes in Form of Chlorophyll-bodies.*

According to Stahl, the chlorophyll-bodies among certain forms of the so-called lower plants (filamentous algæ) are capable of movement. In *Mesocarpus* each cell possesses a *rotating* chlorophyll-plate which bisects the cell longitudinally. In diffuse sunlight the flat surface is turned toward the light, while toward the rays of *direct insolation* a profile position is assumed. In the single-layered leaves of the moss *Funaria hygrometrica* the chlorophyll-bodies assume a position along the lateral walls (profile exposure) in direct sunlight as well as in the dark, while in the ordinary diffuse sunlight they are adjacent to the outer walls (surface exposure). In the palisade-cells of the higher plants it has been observed (mainly according to Stahl) that the approximately hemispherical chlorophyll-bodies with their flattened surfaces directed toward the cell-wall (longitudinal) extend, that is, elongate, somewhat more into the interior of the cell in diffuse sunlight, while in direct sunlight they lie more closely in contact with the cell-wall and increase their diameter in the direction of the adhering surface. Covering a leaf-portion with tinfoil causes this part to become more dark-green as compared with the strongly illumined portions (Sachs).

The following deductions may be drawn from the three phenomena illustrated by the above examples, namely, the rotating of the chlorophyll-plate, and the movements and change in form of the chlorophyll-bodies: 1. Chlorophyll is enabled to derive a maximum benefit from definite light-intensities by enlarging its surface area. 2. It protects itself against light-rays of too great intensity, very probably because it would thereby be injured in its function and composition. According to Pringsheim, chlorophyll is destroyed by concentrated sunlight in the presence of oxygen.

(*c*) *The Chemistry and Physiology of Chlorophyll.*

The exact chemical composition of the green coloring substances designated as *chlorophyll* is but little understood. It contains the elements *C*, *H*, *O*, and *N*; iron is necessary to its *development* (as well as to its composition?). The plasmatic colorless or nearly colorless basal substance (stroma) of the chlorophyll-body is tinged with the green coloring substance; this latter can be extracted with alcohol. The delicate structure of this fundamental substance according to more recent authors is said to be *spongy*, not homogeneous. The fact that chlorophyll-bodies divide has been known for some time. Further, it has been supposed by many authors that two coloring substances, a green and a yellow, are present in the chlorophyll-bodies (according to earlier investigators, blue and yellow). The foregoing statements represent, so to speak, successive stages, which are not yet concluded, of the attempts made to find the chemical and physical structure of chlorophyll-bodies. It is to be kept in mind at present that chlorophyll is a green-colored plasm of highly characteristic properties which manifest themselves in the work of assimilation.

In regard to this *work of assimilation* we must, in view of the results obtained by ENGELMANN (Utrecht), admit that considerable progress has been made. The theory of the physicist LOMMEL that *the rays which are absorbed by the chlorophyll-spectrum* are *most active* in assimilation seems to have been verified by Engelmann. The method of investigation of this latter physiologist is in itself very interesting. It is called the "bacteria method," and consists in its essentials of the utilization of sensitive bacteria suspended in a drop of water. The bacteria accumulate where there is a supply of oxygen. An assimilating cell-thread under the microscope is observed under such environments as expose it to the seven colors of the solar spectrum which are projected side by side on the long axis of the thread; the surrounding liquid contains the sensitive bacteria; they accumulate most at the points of maximum assimilation, hence where the most oxygen is liberated. These experiments show that the *two optima* of assimilation (as judged by the liberation of oxygen) occur first in the *red* and a second smaller *optimum* occurs in the highly refrangible parts of the spectrum: *blue*, *violet*, and *ultra-violet; it is in these spectral areas that the characteristic absorption-bands of chlorophyll lie* (similar to those of living chlorophyll). (The optimum of assimilation in the red [orange] had been observed by REINKE, previous to the investigations of Engelmann, and still earlier by N. J. C.

Müller). All observers agree that assimilation is much less active in the more strongly refrangible half of the spectrum—uniformly designated as "chemical rays" (actinic rays) because they induce certain chemical processes—than in the less refrangible half. The above coincidence of light-absorption and assimilation in the chlorophyll-bodies harmonizes with the supposition[1] that (1) there are certain atomic groups in the chlorophyll which are set in strong vibrations by the red, and less strongly by the more refrangible, rays of the spectrum, and (2) it is these atomic groups which do the work of assimilation *by the transformation of light-waves into chemical activity.* In connection with (1) we might mention the phenomenon that an alcoholic solution of chlorophyll fluoresces with a red light, while the living green plant does not fluoresce; that is, it does not emit a red light, because the necessary vibrations are being transformed into chemical activity. The coloring substance chlorophyll and living plasm work together in the processes of assimilation: chlorophyll acts perhaps after the manner of a ferment.

The history of assimilation also contains the investigations of Pringsheim[2] which created considerable interest at the time. Pringsheim's hypothesis has, according to my knowledge, no firm adherents. The peculiarity of this hypothesis is the original conception that the coloring matter of chlorophyll is only of physical importance, not chemical, and that it is the colorless plasm which is active in assimilation. According to Pringsheim, chlorophyll regulates the respiration of oxygen in plants by the absorption of the so-called "chemical" rays (blue, violet, ultra-violet), so that the activity of such respiration is reduced below the activity of assimilation. The absorption-bands in the red therefore cannot have the significance mentioned above. The optimum of assimilation, according to Pringsheim;—in agreement with Sachs and Pfeffer,—does not lie in the red spectrum but in the yellow. In this matter we are far from having uniformity of opinion. But we will for the time being adhere to the opinion expressed above, which is based upon the results of Engelmann's and Reinke's experiments.

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[1] See Hoppe-Seyler, Botanische Zeitung (1879), p. 819.

[2] Sitzungsberichte der Berliner Akademie, 1879.

We shall now further discuss the process of assimilation.

Each individual chlorophyll-grain may be designated as a workshop of assimilation. The *chief requirements* for this assimilation in the chlorophyll are the presence of CO_2 and the influence of diffuse or direct sunlight. Water is already present in the assimilating cells. Starch[1] (*amylum*) in the form of starch-grains is, in the majority of instances, the rapidly formed product of this assimilation, though it is not the immediate chemical product. Before solid starch-grains can be formed there must be a product of assimilation, also a carbohydrate, which is soluble in water, as some form of sugar; even this may not be the first chemical product. The experimental-physiological fact that there is a volume of oxygen liberated approximately equal to that of CO_2 taken in, is in harmony with the assumption that a carbohydrate is the product of assimilation: $12CO_2 + 10H_2O = 24O + C_{12}H_{20}O_{10}$. According to recent investigations (ARTHUR MEYER), the formation of soluble carbohydrates (devoid of starch) predominates in the chlorophyll of monocotyledons, while starch-formation predominates among dicotyledons. In regard to the *immediate*, still unknown, product of assimilation we may state that, according to the hypothesis of BAYER, CO_2 and H_2O first unite to form an aldehyde (alcohol), and this is polymerized into a carbohydrate ($CO_2 + H_2O = O_2 + CH_2O$). LOEW produced a sugar ($C_6H_{12}O_6$) out of the aldehyde formed from formic acid and limewater.

Under favorable circumstances starch-formation may take place in a few minutes. The starch that is formed will disappear in the dark, also in the light in the absence of CO_2. Among many plants the starch formed during the day is carried into the petiole of the leaf and other tissues during the night.[2]

Chlorophyll-grains as the workshop of our most essential food-substance, bread, deserve special attention. Our present scientific knowledge does not enable us to furnish even an approximate substitute should the above-described chlorophyll activity cease altogether. Science does not even comprehend the chemical methods by which we are so amply supplied with "daily bread." Much less is it capable of imitating the process artificially.

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[1] As a note on microchemistry may be added. Iodine is only slightly soluble in water, more so in solution of KI or alcohol. All these solutions, more particularly the stronger, serve to demonstrate the presence of starch both microscopically and macroscopically by a blue or dark-blue coloration of the starch-grains.

[2] For particulars see the works of SACHS.

Chlorophyll proves to be of great importance during various periods of chemical activity in plants.[1] Among trees with deciduous leaves we see that the assimilating organs are destroyed at the close of the vegetative period. Chlorophyll itself is, however, not simply lost; in the autumn before the leaves begin to fall the most valuable mineral constituents (kalium, phosphoric acid) pass into the enduring portions of the plant, to be again utilized the following year; yellow grains, causing the autumn coloration of so many leaves,[2] remain in the cells of the falling leaves as a waste product. Chlorophyll-grains therefore undergo decomposition.

VII. THE FUNCTION OF AERATION.

The discussion of the fact that gas-forming and gas-requiring processes take place within the cell, and the explanation of a few simple observations associated therewith, will enable us to understand correctly the structural arrangements to be discussed below.

If one considers the fact that air never occurs in the form of bubbles within the active living cell, and that the most important chemical processes (assimilation of atmospheric CO_2 with liberation of oxygen, and true respiration with liberation of CO_2) take place in the living cells, it is natural to conclude that the active exchange of gases which takes place in the immediate vicinity of these cells; or in other words, since no gas appears in the cell in the form of bubbles, that such gas exchange must take place *between* the cells. In fact, the system of aeration of plants is *intercellular*, that is, it is situated outside of the cell.

The aerating system spreads labyrinth-like through the entire plant-body, beginning with the vegetative point at the apex of the stem and extending to the root-tip; beginning with the pith and extending radially, it crosses the wood-parenchyma, cambium, and cortex. In the leaves and other organs it extends to the epidermal tissue, in the form of fine canals. This system among plants living in the atmosphere can be considered only as functional when there are suitable anatomical arrangements to permit the ingress and egress of air. Such anatomical adaptations we find in the stomata (breathing-pores) of the epidermis and in the lenticels of the cork-tissue.

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[1] SACHS, Vorlesungen, p. 384.

[2] These bodies are found in the *cell-sap* of those leaves colored red in the fall.

It will not be found difficult to understand the structural differences between land-plants and water-plants. The supply of air in submerged water-plants is very limited and can be obtained only from the water (absorbed air). Plants temporarily or permanently *partially* submerged are also limited in their supply of air as compared with land-plants. Considerations lead us to the postulate that water-plants must carry a supply of air with them. Comparative observation reveals the following: Every palisade-cell of the leaf of a land-plant which, for example, lies in contact with six other cells is laterally surrounded by six delicate intercellular canals corresponding to the six prismatic corners and edges of each cell; every cubical cell is enclosed by twelve minute canals, etc. Otherwise, comparing the intercellular spaces of land-plants with the air-spaces occurring in the leaves and stems of *water-plants* and *marsh-plants*, it is noticeable to the naked eye that the latter appear as cavities and channels. These contain a large supply of air to satisfy requirements. Such, in one respect, is the interpretation of this phenomenon. The relation between the magnitude of intercellular spaces and the water contained in the surrounding medium was known to older anatomists. The accompanying figure (73) shows a fragment of the parenchymatous tissue of a water-plant (from the leaf of *Acorus Calamus*) magnified about three hundred times. A positive pressure, due to the process of assimilation,[1] has been observed in the air-chambers of submerged green water-plants.

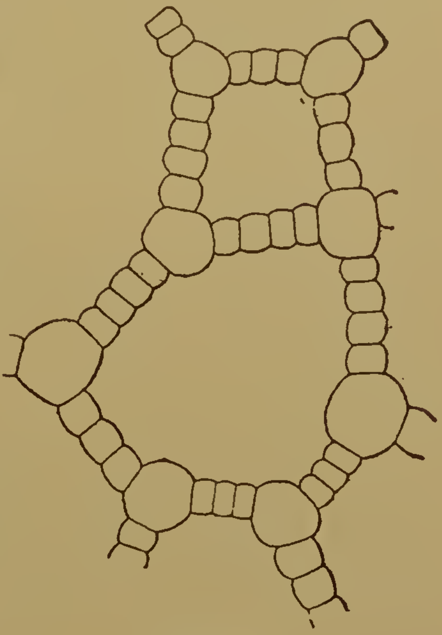

FIG. 73.

Moreover, the air contained in submerged and floating plant-organs tends to reduce the specific gravity of the organs, thus enabling them to float, or at least decreasing the tendency to sink.

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[1] PFEFFER, Physiologie, I. Band, p. 85, *et seq.*

Communication between the intercellular spaces and air-chambers and the atmosphere is brought about by breaks in the continuity of the epidermal covering. Every breathing-pore (stoma, compare Figs. 74–79) is directly opposed to the function of the epidermal system, because it increases the loss of water; the pores *must* remain open at least for a time in order to permit the ingress of CO_2 and the egress of O. The *closing* of stomata is therefore a physiological requirement. This most important requirement will be considered a little later. The unavoidable loss of water is reduced very materially by the facts that the great majority of the stomata of land-plants are on the lower surfaces of the leaves, and in protected positions, as, for example, in depressions; also by being covered with hair-cells, by the elongation of the "entrance," etc. Comparative anatomy reveals a series of instances in which it is possible to know the habitat of a given plant from the position and structure of its breathing-pores. (Concerning this consult TSCHIRCH and other authors.)

Let us add a few further physiological (also teleological in their final results) observations concerning this important apparatus. Submerged and subterranean organs are, in general, entirely free from stomata; for example, they never occur on roots. They occur mainly on green leaves and green stem-organs. It is also worthy of notice that land-plants *devoid of chlorophyll* (saprophytes and parasites) are almost uniformly free from stomata or contain only a few. In bifacial aerial leaves the stomata are, as a rule, on the lower surface, as has already been stated; in floating leaves they occur on the upper surface; in *centric* leaves (not differentiated into luminous sides and shade-sides) they are evenly distributed on all sides. Their number varies greatly: from 40 to 300 per square millimeter. In *Brassica Rapa* there are about 716 per square millimeter. In leathery leaves they are smaller and more numerous; in succulent leaves they are larger and less numerous.

Stomata are organs especially adapted for *closing*. *Lenticels* take the place of stomata when the epidermis is displaced by cork-tissue. Investigation in regard to lenticels shows that the relative permeability to air, at least in some plants, is greater in the spring than in winter. Lenticels are never entirely closed, while the stomata may be. We shall now consider the stomata and lenticels more in detail.

(*a*) *The Structure and Function of Breathing-pores* (*Stomata*).

(With Figs. 74–79.)

Immediately below the *guard-cells* there is a large intercellular space called the *air-chamber* into which the intercellular canals of the surrounding tissue lead. The space at *v* (Fig. 74) is known as "front cavity" (Vorhof, entrance), the one at *h* as "back cavity" (Hinterhof); between them lies the central passage (Centralspalte); *s* are the two guard-cells; *g* the cuticular joint (Hautgelenk); *a* the air-cavity. As a rule, the cuticle covers the wall of the guard-cell about the front cavity, and sometimes extends even to the air-cavity, as shown by SCHWENDENER. The consideration of the mechanics of breathing-pores reveals one of the most interesting accomplishments of modern teleological, or, better, anatomical-physiological, investigations. We shall now briefly consider three main types recognized as such owing to essential peculiarities: 1. *Amaryllis*-type, 2. *Helleborus*-type, 3. *Gramineous* type (according to Schwendener's investigations).

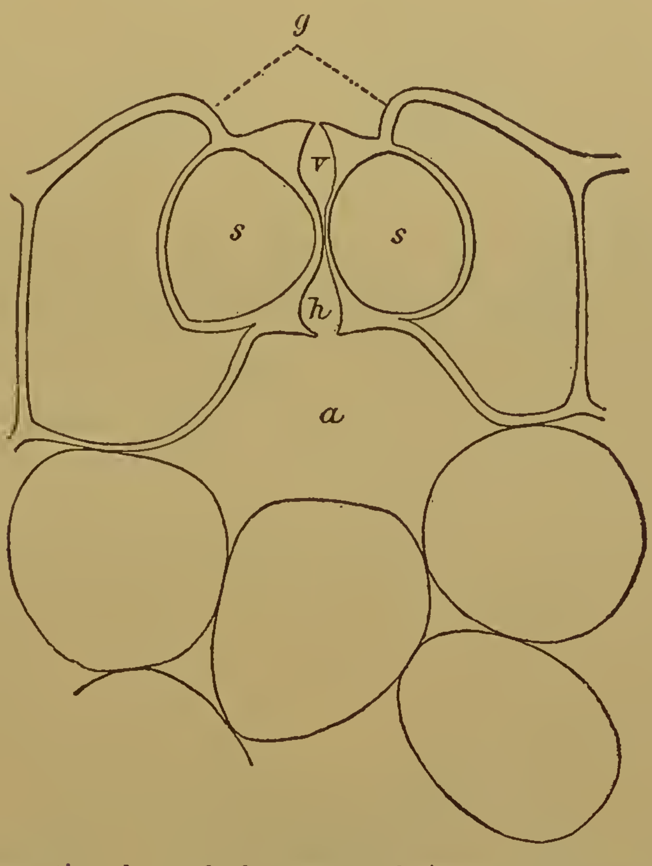

FIG. 74.—Vertical section through the stoma of *Amaryllis formosissima*. Type 1. *a*, Air-chamber. (After Schwendener.)

First type: Amaryllis formosissima and many other plants of widely separated divisions. Volume of front cavity and back cavity variable; large guard-cells, thin opposing walls. Principle: a rubber tube thickened on *one side* bends when pressure is increased in its interior, while the thin wall becomes convex. The thickened portions (ridges of the outer and inner apertures) of the wall of the guard-cell which are nearest each other cause a curvature of the guard-cells when the hydrostatic pressure of the interior is increased. (By the presence of two such thickenings this curvature is much more marked than it would be if only one such ridge were present.) The thin areas of each guard-cell nearest the central passage may permit a hinge-joint movement of the thickened ridges, or by mutual contact they may form a better means of closing the pore than do the thickened ridges. The chief mechanical change involved is the greater expansibility of the thin distal walls as compared with the thick proximal walls.

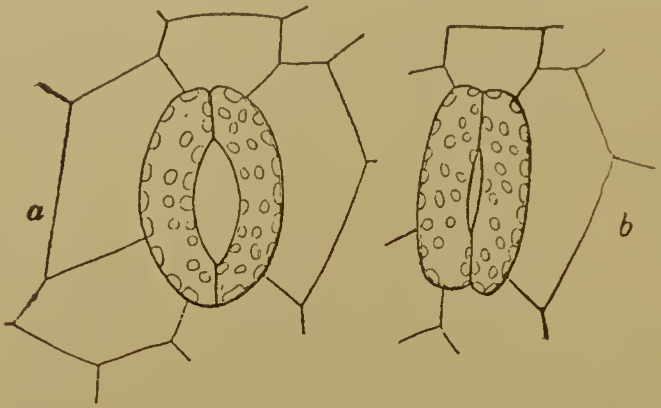

FIG. 75.—Surface-view of an open (*a*) breathing-pore (stoma) and of one closed (*b*). (Diagramatic.) Illustrating types I and II.

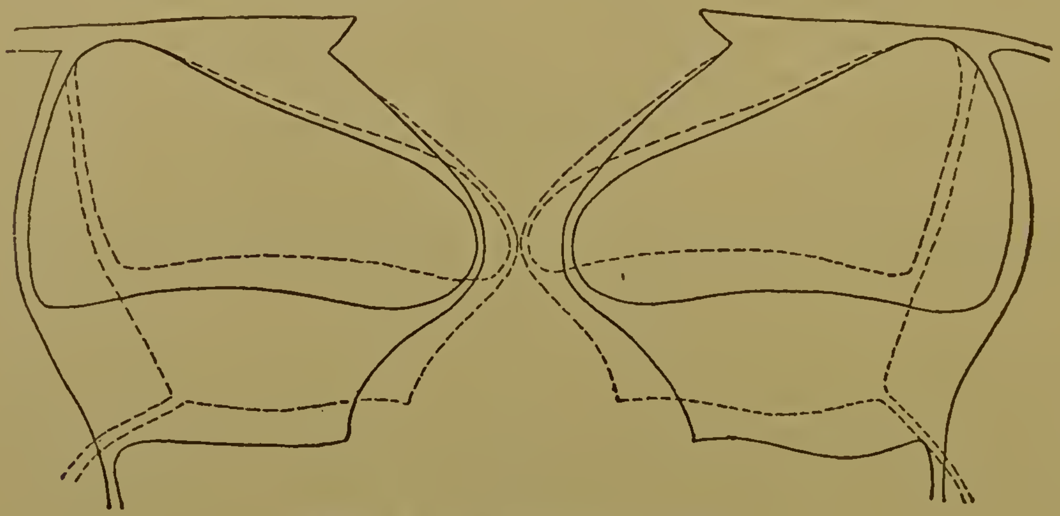

FIG. 76.—*Helleborus.* Type II.
(After Schwendener.)

Second type: Helleborus. Front cavity immovable, back cavity undergoing great changes in size and position. The changes in form of the lumen of the guard-cell as seen in cross-section are such that in the non-turgescent state the outline of cell-wall presents the form of a *scalene triangle*; in the turgescent state it assumes more nearly the form of an *isosceles triangle* (see Fig. 76). Chief mechanical change: hinge-joint movement of the thin areas of the guard-cells near the central passage accompanied by a similar movement of the distal wall near the cuticular joint. The entire guard-cell may also become curved. There will be no difficulty in finding forms intermediate between the first and second types.

Third or *Gramineous type.* The frequently much-elongated middle portion of the guard-cell is thick-walled and passive. The lumen of the guard-cell in cross-section through the middle presents the appearance of a wedge placed transversely (Fig. 77). The movements due to turgor are manifest in the expanded thin-walled lower ends (subsidiary cells) of the guard-cells (Figs. 78 and 79). The open central passage (stoma) is bounded by parallel straight lines, formed by the outline of the above-mentioned middle portions of the guard-cells (Fig. 79). The subsidiary cells (*n*) perform the function of 1, a "membranous hinge" similar to the thin cell-wall areas of the other types; 2, in a few instances, verified by experiment, they assist in closing the pores during the turgescent state, since the central pore has been observed to remain open even after the subsidiary cells and *guard-cells* were killed.

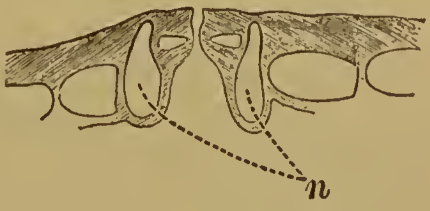

FIG. 77. — Vertical section through the stoma of *Carex leporina.*
(After Schwendener.)

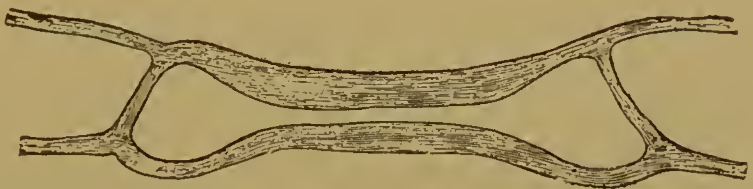

FIG. 78.—Radial longitudinal section through a guard-cell of *Triticum.*
(After Schwendener.)

The exceptions referred to under type II. are not contradictory of the following general statement: *Increasing turgescence of the guard-cells is the force which causes the opening of the pores, and,* *conversely, reducing the turgescence of the guard-cells tends to close the pores.* Besides this general statement, a few special considerations are necessary. It has been observed that the stomata of some water-plants are open at all times whether the guard-cells are turgescent or not. It must also be remembered, as has already been stated, that the subsidiary cells in some cases assist in closing the breathing-pores. The opening of pores is also influenced by the pressure of the epidermal cells.

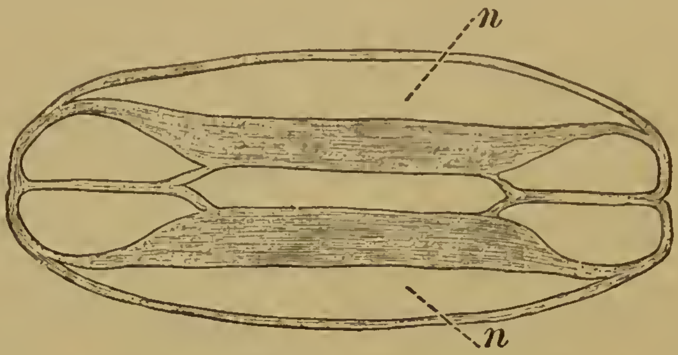

FIG. 79.—Surface-view of a breathing-pore of *Triticum vulgare.* Type III. (Open.)
(After Schwendener.)

Why does the turgor of the guard-cells increase? First of all *sunlight* is the outer agency which produces these changes. It is evident also that the chlorophyll of the guard-cells enters as a factor in turgor. *The presence of chlorophyll is characteristic of the guard-cells in contradistinction to the other epidermal cells.* The delicate structure or other peculiarities of the guard-cells are of importance in facilitating diosmosis with neighboring epidermal cells (gymnosperms).

The question whether warmth has an effect similar to that which light produces could not be satisfactorily answered by SCHWENDENER, although he does not doubt that suddenly reducing the temperature to zero reduces the turgescence of the guard-cells, while raising the temperature increases it.

The mechanism of the coniferous type is still under investigation.

(*b*) *Lenticels.*

A knowledge of these structures presupposes a knowledge of cork-tissue. Lenticels are lense-shaped cork-like tissue-formations of the bark which have the peculiarity of always being traversed by intercellular spaces. Little is known concerning these organs in monocotyledons. Among dicotyledons and gymnosperms they originate from the cork-cambium, and consist either of entirely suberized cells or sometimes also of such as are not suberized; both cell-forms contain intercellular spaces radially arranged corresponding to their succcession in development.

Very frequently lenticels are sufficiently large to be seen by the naked eye, for example, in the birch. Their permeability to air has already been referred to. Their origin does not always coincide with the position of a breathing-pore; very frequently lenticels are formed after bark-formation has begun. (KLEBAHN, who continued the investigations begun by STAHL and others, has studied lenticel-formations more particularly.)

VIII. THE FUNCTION OF ROOTS.

We shall discuss: 1, the activity of ordinary or *subterranean* roots, and 2, that of *aerial* roots. Their internal anatomical structure (the transit-cells in the protective sheath, etc.) has already been discussed.

(*a*) *Subterranean Roots.*

From the fact that the absorption of food is to be accomplished by closed cells it is easy to comprehend that such food-substance must be in a soluble (capable of osmosis) form. Water and watery solutions of mineral substances whose chemical composition and nature will be considered elsewhere are of special importance. The portion of the root which serves the purpose of taking up the food-substances is comparatively small; it is located behind the root-cap and is considerably increased in surface by its numerous *root-hairs*. In *young* roots the portion bearing the root-hairs comprises, in general, the greater portion of the entire root-surface exclusive of the very tip, in older roots only the portion immediately behind the root-tip (see Fig. 80).

Transverse septa are wholly wanting in the root-hairs, branching rarely occurs, so that they represent long papillose outgrowths of the epidermal cells (Fig. 81). The absence of transverse septa, the thinness of the cell-wall, the irregular curvatures—all serve the specific purposes of root-hairs, namely, to bring them in contact with water and particles of soil, to enable them to take up and conduct food-substances in solution. Other substances not soluble in water are rendered capable of being taken up by the root-hairs. Some mineral substances are made soluble by a secretion of the root itself, perhaps an *organic acid.* According to SACHS, this may be demonstrated by means of a polished marble plate, osteolith- or dolomite-plate, upon which growing roots produce figures of corrosion. Blue litmus paper is turned red by this excretion of the roots. The activity of the root-hairs also reduces or entirely removes certain salts from the soil, as lime-salts, phosphates, and compounds of ammonia. Besides the organic acid referred to, roots also secrete CO_2.

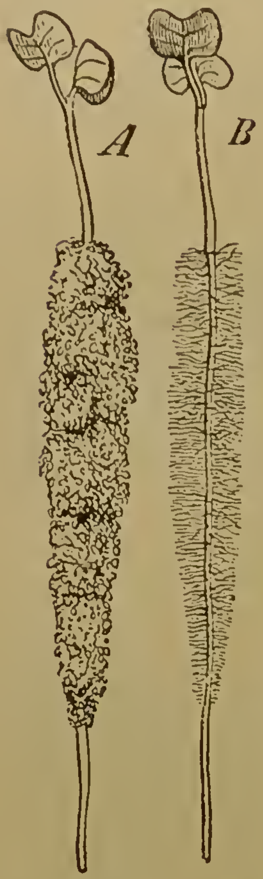

FIG. 80. — *A*, A young seedling with particles of soil adhering to the root-hairs. *B*, The same with soil-particles washed away. (After Sachs, from Frank.)

In plants devoid of roots the soluble food-substances are taken up by the *rhizoids*, hair-like structures met with among the prothallia of ferns, and among the lichens and mosses. In *Marchantia* these hair-like rhizoids possess peculiar elevated thickenings of the cell-wall which project inward; they have perhaps a mechanical function, namely, to prevent collapse of the cells.

(*b*) *Aerial Roots.*

In the plants of moist warm climates—a condition artificially produced in our greenhouses—roots very frequently develop from aerial organs. Such roots may subsequently enter the soil, in which case the subterranean portion performs the function of an ordinary root; or they may remain permanently suspended in the air, in which case they are specially organized to serve as aerial organs (*Aroideæ*, epiphytic orchids). In the anatomy of true aerial roots there is found just outside the normal root-cortex a covering of several cell-layers in thickness called the *velamen.* The cells of this layer are filled with air and the walls contain delicate spiral or reticular thickenings. The special function of this cell-layer is to *absorb water-vapor.* Between the velamen and the cortex there is a layer of cells which is known as "endoderm;"

this name suggests its similarity to the protective sheath (endoderm) of ordinary roots. In it are found passages to the internal parenchyma (LEITGEB)[1] which no doubt serve to conduct moisture to the interior. The outermost cells of the velamen may develop hair-like structures, especially when the growing root lies in contact with a solid moist body.

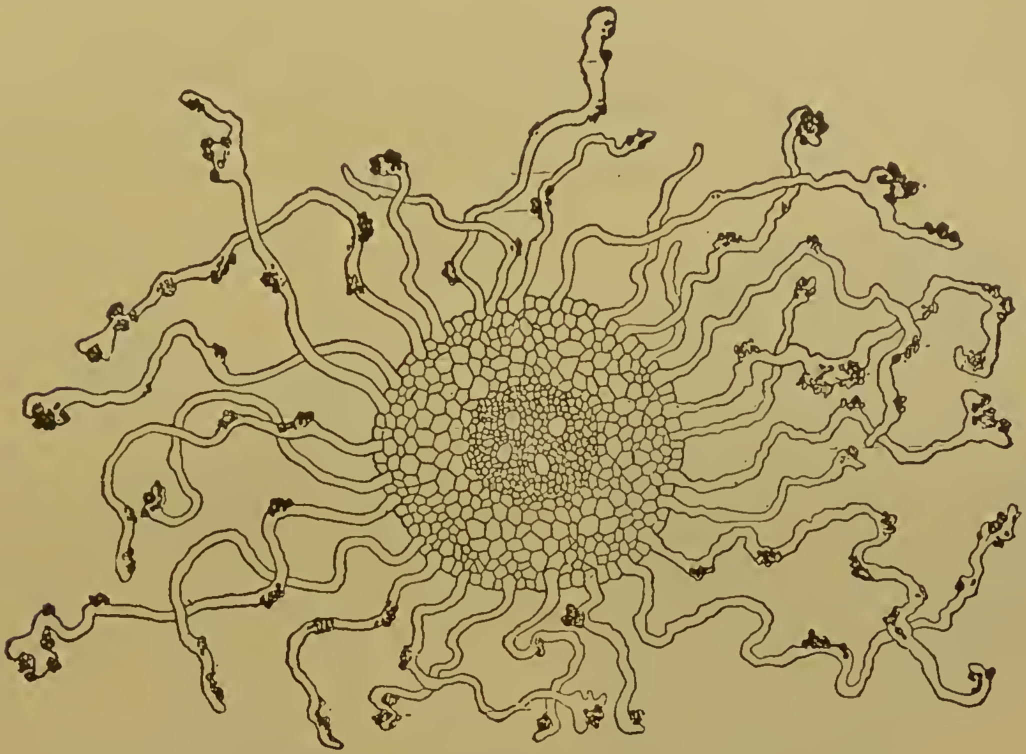

FIG. 81.—Cross-section of a root with root-hairs.
(After Frank.)

IX. THE APPROPRIATION OF ASSIMILATED FOOD-SUBSTANCES.

In order to form a correct conception of the processes of nutrition which are about to be considered it is necessary to have a clear understanding of carbon-assimilation (see pp. 128 *et seq.*). It is true that the mass of solid food-substances and increase in the weight of plants can be traced to the disintegration of atmospheric CO_2 by the green organs; but plant-life in its various conditions and conformations presents a series of phenomena which occur as regularly as the process of assimilation, and which teach us that the appropriation of food-substances *already assimilated* is an essential part of plant-nutrition. Of the four important conditions coming under this heading three are widely distributed and shall receive our immediate attention.

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[1] This investigator (1864) made a special study of the aerial roots of orchids.

(a) *Condition of Seeds before the Beginning of Assimilation.*

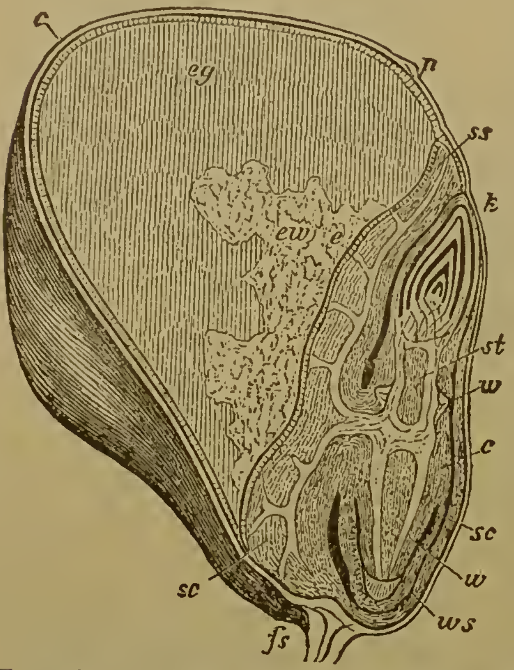

FIG. 82.—Longitudinal median section through the seed of *Zea Mays*. **c**, Epidermal layer; *n*, point of attachment of the style; *fs*, base of the ovary; *eg* compact and *ew* less compact portion of the endosperm; *sc* and *ss*, *scutellum* (absorbing organ) with epidermis *e*; *k*, young leaves; *st*, first internode of the stem; *w*, main root; *w′*, lateral roots springing from the stem; *ws*, root-sheath. (After Sachs.)

The undeveloped embryo, which, when mature, becomes separated from the mother-plant, receives a greater or lesser supply of stored food-substances during its attachment to the mother-plant, which serve as the initial food-supply during germination. This is very marked in our cereals. The mass of the grain consists of stored food-substance, the starch-bearing *endospermous tissue*;[1] the small embryo (see Fig. 82) is situated at one side. We may obtain a better summary of various seed-structures by separating them as to their composition and mode of appropriating or reabsorbing the stored food-substance.

1. The embryo possesses a special flat shield-like organ ("scutellum") whose function it is to absorb the food-substances of the endosperm. This organ sometimes develops papillæ-like projections, which penetrate the endosperm-tissue in order to facilitate the absorption of the food-material (grasses; see Fig. 82).

2. Among certain palms there is a wart-like apical portion of the cotyledon which serves to absorb the food-material.

3. The cotyledons themselves are very frequently the bearers of the reserve food-substance; examples: *Quercus*-seeds, beans, peas, lentils, etc. In the beginning the cotyledons are fleshy, subsequently they shrink, as the food-material is removed during germi-

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[1] In this case the expression "seed-albumen" is chemically incorrect, since the substance consists essentially of a carbohydrate.

nation (Fig. 83). Strictly considered, this is really a case which serves for the circulation and utilization of the assimilated food-substances in one and the same plant, and not for the appropriation of food-substances from the outside.

4. The cotyledons at first serve as organs to absorb the endosperm, and subsequently become organs of assimilation (see Fig. 84, which represents a seedling of *Pinus Pinea.*)

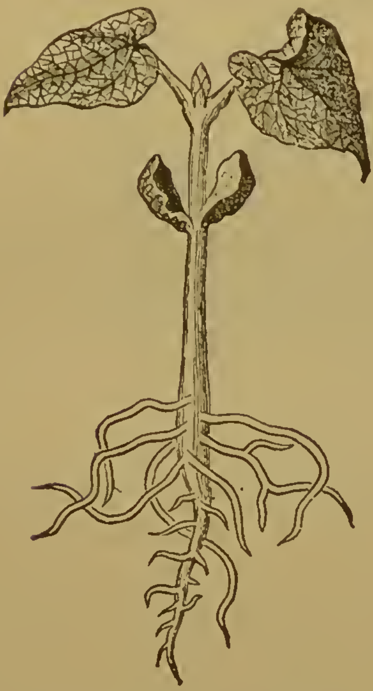

FIG. 83.—Bean-seedling. (After Krass and Landois.)

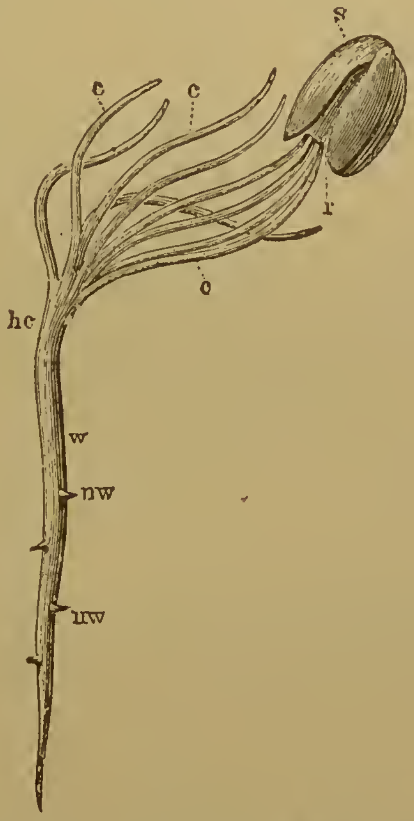

FIG. 84.—Seedling of *Pinus Pinea.* *w* and *nw*, Roots ; *c*, cotyledons ; *hc*, hypocotyledonous stem (radicle); *s*, outer seed-coat; *r*, inner seed-coat. (After Berthold and Landois.)

5. The cotyledons contain some food-material and begin the function of assimilation as soon as the reserve food is assimilated. The endosperm is wanting. The cotyledons soon become green (*Cruciferæ*). This case, like number 3, is introduced for the sake of completeness.

(*b*) *Nutrition of Saprophytes and Parasites.*

The term "parasite" in itself indicates that the organisms referred to require an organic substratum upon which to live. The assimilation of food-substances prepared by *life-processes* is common to both *saprophytes* and *parasites*. If the food-supplying organism is alive and injuriously affected by such a relation, it is recognized as *parasitism*. Vegetable parasites are either endophytic or epiphytic, that is, either growing within the plant or attached to the outer surface. If the organic substances belong to *dead* organisms, the organisms living upon them and taking nourishment from them are known as *saprophytes*. Theoretically these groups may be clearly separated, but actual observation teaches that the two modes of life-activity may become interchanged or may occur side by side.

Fungi are entirely dependent upon organic food, since they contain no chlorophyll. In the numerous fungi which infect living plants, but which can only reach their maximum development on dead plants, parasitism and saprophytism seem to alternate.

The few phanerogams devoid of chlorophyll are also dependent upon assimilated or organic food; for example, the orchid *Epipogon Gmelini* is a saprophyte, *Cuscuta* is a parasite; *Monotropa* is said to be both parasitic and saprophytic. *Viscum album*, the well-known mistletoe, is evidently parasitic, although its green leaves have the power of assimilation; *Neottia nidus avis* is a saprophyte and has some power of assimilation owing to the chlorophyll in the reduced scaly leaves.

Parasitic phanerogams present remarkable anatomical arrangements, which enable them to take up assimilated food-substances. The details of this adaptive arrangement were studied by Solms-Laubach, and L. Koch. There are three characteristic parts to the organ which serves to absorb the food-substances; namely, the *haustorium*, the *sucker*, and the *absorbing-cells*. These are shown in figure 85, *A* and *B*. *B* represents the absorbing cells, *s* the sucker somewhat magnified; *w* is the root of the host-plant.

In regard to the parasitic fungi which have the power of penetrating cell-walls, it is to be noted that this phenomenon is associated with the excretion of ferments having the property of dissolving suberized as well as unsuberized cell-walls. To the *Schizomycetes* (bacteria) especially, various fermentative activities are ascribed, not only for the purpose of dissolving cell-membranes but also for dissolving albuminous substances. The fact that chlorophyll-bearing plants occur parasitically on rhizomes and roots of other plants very probably indicates that they are partially dependent upon a nitrogenous food-supply.[1]

The following substances serve as food for bacteria and moulds: the carbohydrates, various organic acids, glycerin, albuminous substances, peptone, leucin and asparagin. These substances and many others were used by PASTEUR, and NÄGELI in numerous culture-experiments.

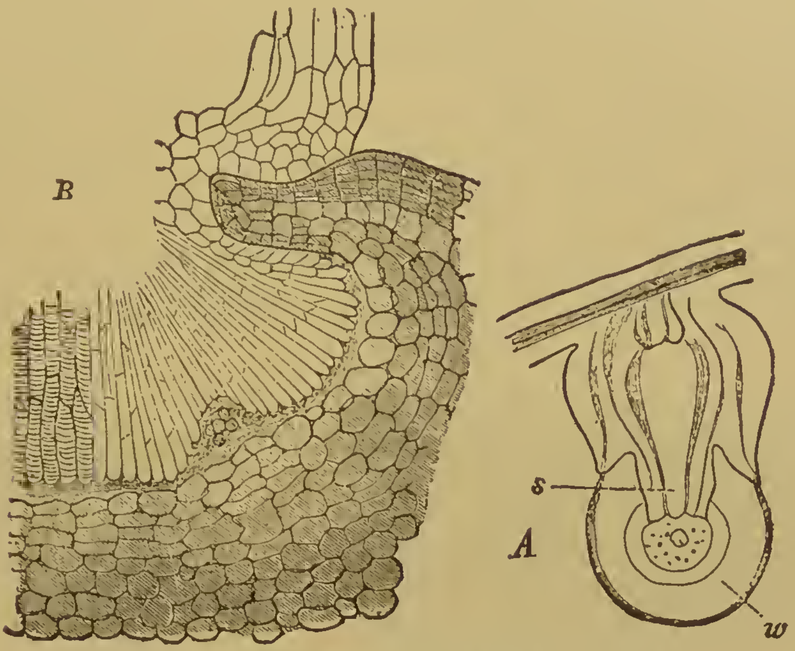

FIG. 85.—Haustorium of *Thesium pratense.*
(After Solms-Laubach.)

(c) *Symbiosis.*

Externally symbiosis resembles parasitism in that it represents the organic union of one plant with another. On closer examination, however, we notice a marked difference. In the definition of parasitism it was stated that the host-plant was in some way injuriously affected. In symbiosis two plants live together as in parasitism, but they *mutually assist each other in their life functions, especially in nutrition.* The term symbiosis was introduced by DE BARY in his work entitled "Die Erscheinung der Symbiose," published in 1879.

The most important example is met with in *lichens* (Figs. 86–88), the true nature of which was made known by SCHWENDENER's epoch-making researches (1860–1870). Other important researches in the same line were carried on by BORNET, DE BARY, STAHL,

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[1] PFEFFER, Pflanzenphysiologie.

Reinke, and others, some before and some after Schwendener. Lichens predominate in the colder climates, where they frequently cover large areas of soil; in our zone they occur on trees, rocks, etc., in the form of crustaceous, foliaceous, or fruticose growths. The chlorophyll-bearing algae ("gonidia") perform the assimilating function of this consortium, while the fungus, which usually constitutes the greater bulk of the lichen-body, serves to take up water and watery solutions and to form the attachment to the substratum (by means of rhizoids), and has also the function of sexual reproduction.[1] Rees and Stahl have observed the development of the thallus of a lichen by the artificial synthesis of an alga and a fungus. Fig. 86 shows the anatomical structure of the thallus of a foliaceous lichen as seen in cross-section: *o*, upper cortical layer; *u*, lower cortical layer; *r*, rhizoids; *m*, medullary layer; *g*, algal layer (gonidial).

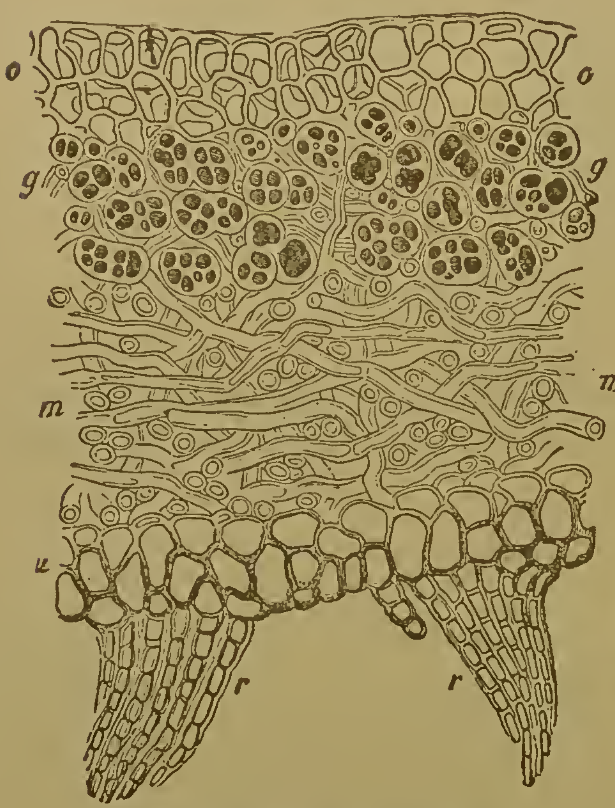

Fig. 86.—*Sticta fuliginosa.* (× 500.) (After Sachs.)

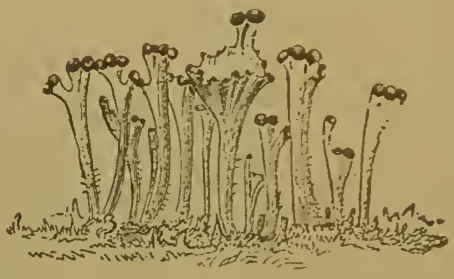

Fig. 87.—*Cladonia cornucopioides.* (After Berthold and Landois.)

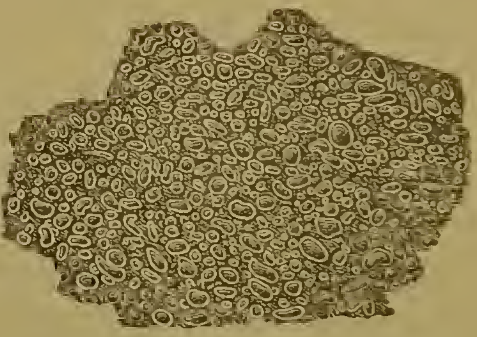

Fig. 88.—*Parmelia parietina.* (After Krass and Landois.)

Again and again a tendency manifests itself among certain investigators to point out "unsuitable" conditions and relations in plant-life, as, for example, plant-diseases produced by parasites. There are also minds which cannot understand how such pathological changes can be harmonized with the original perfection of the vegetable creation. Let such direct their attention to the above facts of symbiosis, which show that conditions which at first sight resemble parasitism are in fact beneficial to both plants. Epiphytic and endophytic association of plants does not in all instances bear the stamp of the pathological or unsuitable. Furthermore, it is in perfect harmony with the Christian conception of creation that the arrangements in nature no longer possess their highest perfection. The injurious and pathological has no doubt made its appearance *secondarily*, and was not originally introduced. The teleological view of nature is not obscured by the erroneous conception of parasitic phenomena in the plant-kingdom, nor by the narrow affirmation that diseases of man cannot be harmonized with the doctrine of the omnipotence of an all-wise Being.

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[1] Lichen-spores are very probably not sexual products. Stahl's observations on *Collema microphyllum* have not yet been verified.—Trans.

There is a very remarkable phenomenon of general occurrence, which is doubtless a form of symbiosis, the more correct knowledge of which we owe to various investigators, especially to Frank. This is the *mycorhiza* (fungus-root) of certain trees. In all climates the terminal root-portions of certain forest trees, as *Cupuliferæ*, *Betulaceæ*, *Coniferæ*, are covered with hyphæ of some fungus ("ectotrophic mycorhiza") which perform the function of root-hairs and also take up food-substances from the soil. The biological interrelation has as yet not been explained very satisfactorily. In reference to Fig. 89 it should be stated that higher magnifications of a longitudinal section shows that the hyphæ of the fungus (*m*, *s*, *m*) actually surround the epidermal cells of the root.

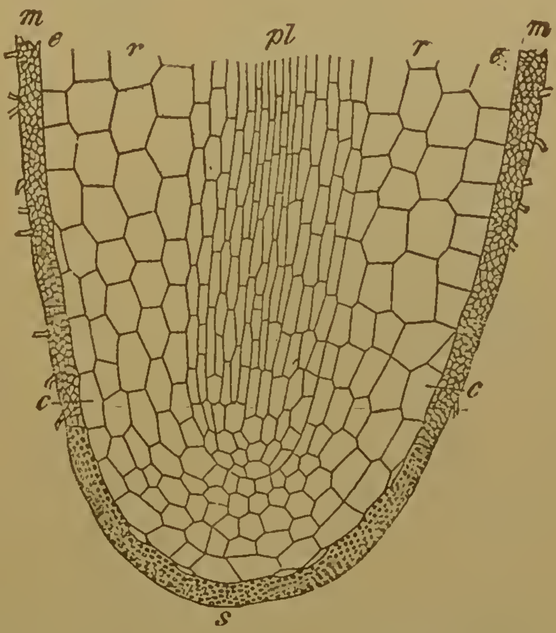

Fig. 89.—Root-tip of *Carpinus Betulus* with *mycorhiza*. (After Frank.)

Here also must be added the "endotrophic" mycorhiza of the *Ericaceæ*, etc., as well as the symbiosis in the swelling of the roots of *Elæagnaceæ* and *Myricaceæ*, and finally the well-known root-tubercles of *Leguminosæ*. The latter are neo-formations from the root itself *caused by and inhabited by* fungi (bacteria, rhizobia). The formation of these tubercles can be prevented only by previously sterilizing the soil, for example, at 100° C. moist heat or at higher temperature of dry heat; from this we conclude that the tubercle-producing organisms are generally distributed in the soil. At certain times, such as near the close of the vegetative period or during lack of moisture, the leguminous plant digests and assimilates the greater part of the infecting bacteria, while a small number escape from the decaying tubercles and subsequently enter other roots.[1]

According to the observations of BECCARI, FRITZ MÜLLER, DELPINO, and A. F. W. SCHIMPER, *plants* and *animals* may associate in symbiotic relations. The investigators mentioned made observations on the reciprocal relations between *ants* and *plants* in tropical America, communicated by Schimper in 1888. Strictly speaking, this subject does not come within the scope of the present work, yet it has some bearing on true symbiosis, and for that reason will be briefly treated. A certain species of ant lives upon and obtains its food from the branches of a tree (*Cecropia*); in return the ants protect the tree from the injurious and destructive attacks of another species of ant. These "myrmecophilous" trees have a hollow stem transversely divided into chambers; each chamber contains an opening leading to the exterior through which the ants, move in and out. This opening is made by the protecting ants which eat away a thin lateral septum. On the lower surface of the petiole there are small pear-shaped bodies rich in albumen and fatty oil. These drop off very easily, but others are continually formed and serve as food for the protecting ants.[2]

(*d*) *Insectivorous Plants.*

We have seen that plants take up assimilated food, that roots excrete acid for the purpose of dissolving particles of soil; to these and similar phenomena we shall add another which has been observed in about fifteen species of plants, that is, the digestion of animal substance by plants. The most interesting features of these "insectivorous" plants are the specific arrangements for the capture of living insects.

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[1] The literature on this subject is very voluminous. FRANK in his Lehrbuch der Botanik (1893) gives the more important conclusions, also the more important citations, of the literature.

[2] Various myrmecophilous plant-species with different species of protecting ants have also been observed and collected in South America by Dr. H. H. Rusby.—TRANS.

Our indigenous genus *Drosera* shall first be cited as a typical example (Fig. 90). Small insects adhere to the sticky substance excreted from the glandular enlargements of the "tentacles" (trichomes) covering the margin and the entire upper surface of the leaf. The pressure of the insect acts as a stimulus which is conveyed from tentacle to tentacle, until finally all the tentacles incline toward the middle of the leaf (Fig. 90, *e*). The insect dies and the albuminoid portion is dissolved by a copious secretion from the many-celled glandular structures which acts similar to the gastric ferment pepsin.[1] The chitinous skeleton remains unchanged and is finally discarded. The dissolved substances are taken up by the leaf, and the trichomes resume their normal irritable position. In *Dionaea* the glandular hairs secrete the ferment and the acid only after they have been irritated. In the leaves of *Nepenthus* (Madagascar) the ferment is secreted without any mechanical stimulus, while the secretion of acid is due to the presence of a chemical stimulus. In the case of *Drosera* it remains a question whether or not the ferment is secreted without the presence of a stimulus. It is believed that the appropriation of animal food by some insectivorous plants (*Dionaea* and *Aldrovanda*)

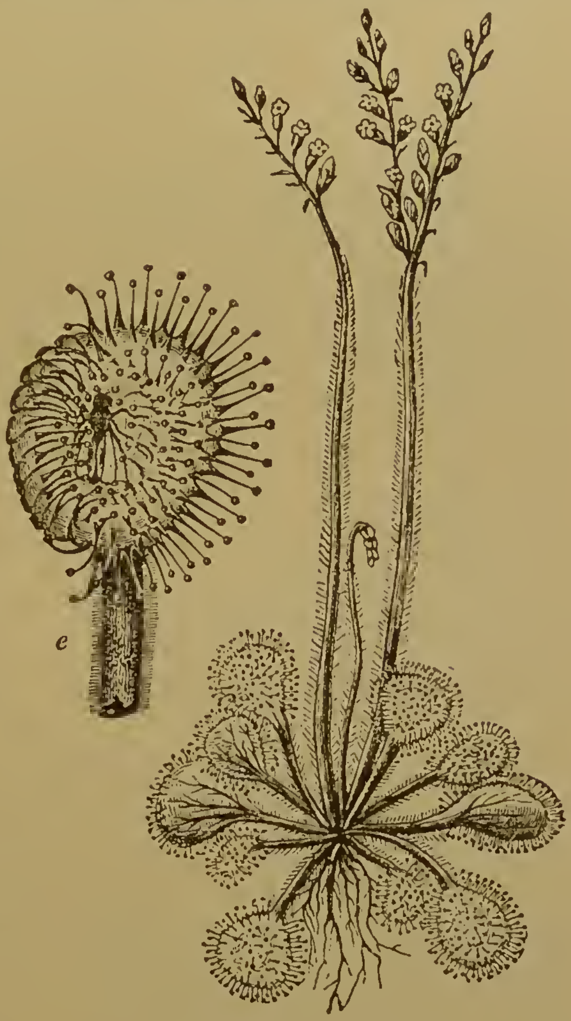

FIG. 90.—*Drosera*.
(After Krass and Landois.)

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[1] According to recent investigations this digestive ferment is secreted by bacteria living on the plant.—TRANS.

is only facultative.[1] Conclusive results have not yet been obtained in regard to other species. (It must also be borne in mind that there are many investigators who deny that green plants can assimilate animal food.—Trans.)

X. THE STORING AND FUNCTION OF RESERVE MATERIAL.

(*a*) *Storing of Water.*

The epidermal water-supplying system ("aqueous tissue") acquires such thickness in some plants (*Piperaceæ*, *Bromeliaceæ*) that it evidently not only serves as a water-bearing covering, but also as a reservoir for water. Some internal aqueous tissues also belong here. For example, in the leaf of some species of *Aloe* an internal water-bearing tissue is enclosed by the assimilating tissue. In such orchids as are especially adapted to withstand great dryness *isolated water-cells* (idioplasts) are found distributed through the assimilating tissue. These reservoir-tracheids have fibrous thickenings of the wall which prevent the collapse which would be caused by the excessive hydrostatic pressure of the surrounding cells. One of the typically xerophilous plants, *Mesembryanthemum crystallium*, is supplied with enlarged epidermal cells occurring in the leaf and petiole, which are filled with water. During excessive dryness the plant receives its supply of water from these cells. In some extreme cases of the development of water-tissue the water contains a large percentage of saline substances in solution which reduce transpiration. In xerophilous grasses (*Eragrostis*, *Cynodon*) it has been observed that the leaves become alternately broader or narrower according to the amount of water present. This is due to the fact that the lamellæ of the water-tissue alternate with the lamellæ of the assimilating tissue; the former shrink on the loss of water, thereby reducing the width of the leaf. In still other cases there is a folding and unfolding due to similar changes within the so-called "hinge-cells" (Tschirch).

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[1] Pfeffer, Über fleischfressende Pflanzen, etc., Landwirtschaftliche Jahrbücher, 1877.

(*b*) *The Storing of Starch and Other Food-substances, Especially the Albuminous Substances.*

Entire organs and complexes of organs, even entire plants, have at times the character of reservoirs for reserve materials. Parenchyma, medullary rays, cortical tissue, and especially the woody tissue of trees during winter, may serve as storage-tissue.

Sometimes nitrogenous (especially albuminous) and non-nitrogenous (carbohydrates, fatty oils) substances occur in one and the same tissue. Protoplasm and starch occur in the potato, protoplasm and dissolved sugar in the beet, protein-granules (albumen) and starch in the cotyledons of beans, peas, and lentils. In other cases the reserve carbohydrates occur in the form of cellulose: thick-walled cells with numerous pores form the storage-tissue of *Fritillaria imperialis*, of the date-palm, of *Phytelaphas macrocarpa* ("vegetable ivory"), and of *Coffea arabica*. In most of our grasses albumen and carbohydrates occur separately in different tissues; the cereals contain a peripheral layer bearing protein-grains (gluten-bearing layer), while the mass of the storage-tissue contains the starch and a small amount of protein (Fig. 91).

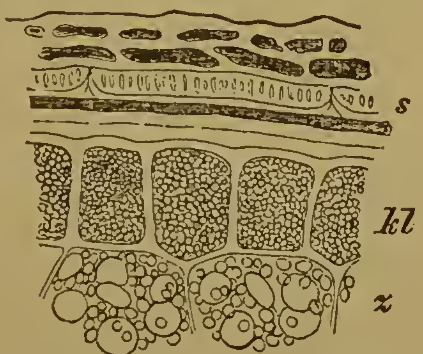

FIG. 91.—Section of the peripheral portion of a grain of wheat.

s, Seed-coat; *kl*, gluten-bearing layer; *z*, starch-bearing endosperm-cells. (× 300.) (After Haberlandt.)

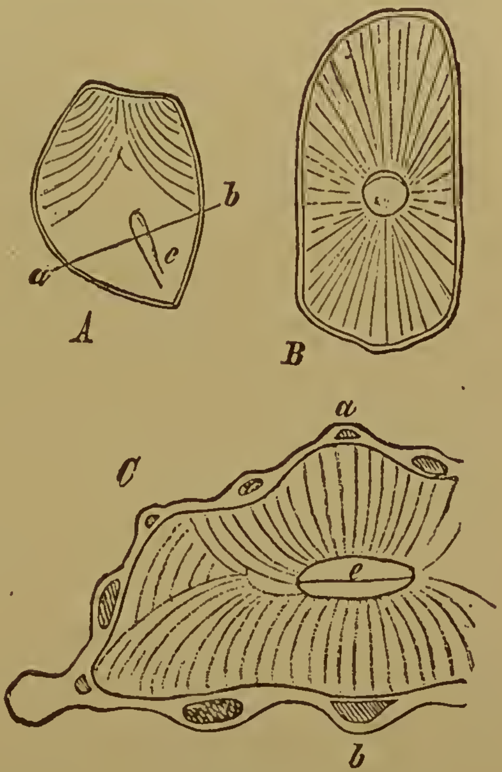

FIG. 92.

A, *Iris*-seed in tangential longitudinal section. *B*. Cross-section of the same in the direction *ab*. *C*, Seed of *Anethum Sova* in cross-section. The arrangement of the endosperm-cells is indicated by the lines. (Schematic.) (After Haberlandt.)

The storage-cells are sometimes strikingly arranged in straight rows or in curves. Such arrangement may be dependent upon mechanical or physiological requirements. The mechanical principle is very evident from the fact that the cell-rows are arranged along the lines of greatest tension (Fig. 92).

When the seed of *Anethum Sova* (Fig. 92, *C*) swells during germination, it increases considerably (28 per cent) in the diameter *ab*; in this diameter there is also a maximum pressure of the soil; the diameter in the horizontal direction increases only 11 per cent. The tangential-longitudinal section of *Iris*-seed shows the *mechanical* curves. In cross-section we see these lines radiate from the embryo, where they are evidently of physiological, not mechanical, significance. HABERLANDT has made a special study of storage-tissues and the mechanical and physiological arrangements just referred to.[1] In mytreatment of this subject I have adhered to Haberlandt's interpretations.

XI. SECRETION.

The products of plant-metabolism which *cannot be further utilized in the plant-economy*, and which do not form a part of the cell (as, for example, the cell-wall), are, in general, designated as *secretions*. In this collective noun I include *secretions in the narrower sense* as well as *excretions*.[2]

We may designate all those products formed from special organs—the organs of secretion, or glands—as secretions, in the narrower sense. "Excretion" is not the product of a specific organ; the waste material collects in certain cells not united to form a distinct structure, while true secretion is invariably associated with an apparatus marked by specific anatomical peculiarities (HABERLANDT).

Our imperfect chemical knowledge of the subject does not permit us to give any detailed description of the phenomena under consideration. We shall briefly consider secretion *in general*.

The saccharine solution in the nectaries of flowers, the resin of conifers, the etherial oils, many of the formations of calcium oxalate, the tannin in many cells, and the water of transpiration are all products not required in further metabolic processes.

We can see the utility of many of these substances and their great importance in plant-life; therefore secretion does *not* imply a useless product. It is also evident that a substance, as sugar, may be a secretion in one part of the plant, and in another part it may be a plastic substance.

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[1] HABERLANDT. Physiologische Pflanzen-Anatomie.

[2] *Ibid.* p. 320.

Concerning the physiological significance of many secretions, it may be mentioned that the sweet secretions of the nectaries and the etherial oils are of importance in cross-fertilization, due to the attraction they have for the appropriate pollen-bearing insects. The sticky secretion of the stigma serves to retain the pollen as well as to aid in the formation of the pollen-tube. Resinous secretions serve to cover and protect injured parts. Certain sticky secretions from superficial glands serve to keep off injurious crawling insects (KERNER). According to STAHL,[1] the acicular bundles of calcium oxalate which occur so frequently in various tissues serve as a protection against animals, particularly snails, that attempt to feed upon the plants; tannin serves a similar purpose. Sticky resinous secretions sometimes unite the bud-scales (in winter) and protect them against moisture and decay. Waxy coatings (example of useful excretion) reduce the transpiration and evaporation of moisture. The secretions of insectivorous plants must also be included here.

The translucent spots on many leaves frequently indicate the location of glandular structures, mostly *internal* glands as distinguished from *external* glands; two examples of the latter are shown in Fig. 93. Besides the external and internal glands, we shall refer more particularly to the duct-like secreting organs. The resin-ducts of conifers (they occur in the wood, bark, and leaves), the oil-ducts of the *Umbelliferæ*, and the resin-ducts of *Cycas* may be mentioned as the more important examples.

Of the "excretions" there are receptacles containing a mucous substance; again we find cells more or less filled with resin or oil, receptacles bearing tannin or crystals, also the so-called "cystoliths" occurring in *Ficus*. Receptacles for mucus occur in the *Malvaceæ*. In the *Aroideæ*, *Compositæ*, and *Convolvulaceæ* we find resin-bearing tubes resembling the laticiferous tubes (DE BARY).

In agreement with DE BARY[2] I wish to emphasize that not all secreting organs are the result of cell-fusion; many of them are intercellular ducts and chambers. If they are formed by the crowding apart of cells, they are said to be formed according to the "schizogenous" method. Example: the resin-ducts of conifers.

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[1] Pflanzen und Schnecken, 1888.

[2] Comparative Anatomy.

If they are the result of the solution or disorganization of cells, they are said to be formed by the "lysigenous" method, or "rhexigenous" when the cells are torn. In the lysigenous form the secretion appears in the individual cells; subsequently the cell-walls are dissolved and the products of secretion flow together. Example: the oil-bearing epidermal glands of *Dictamnus Fraxinella.*

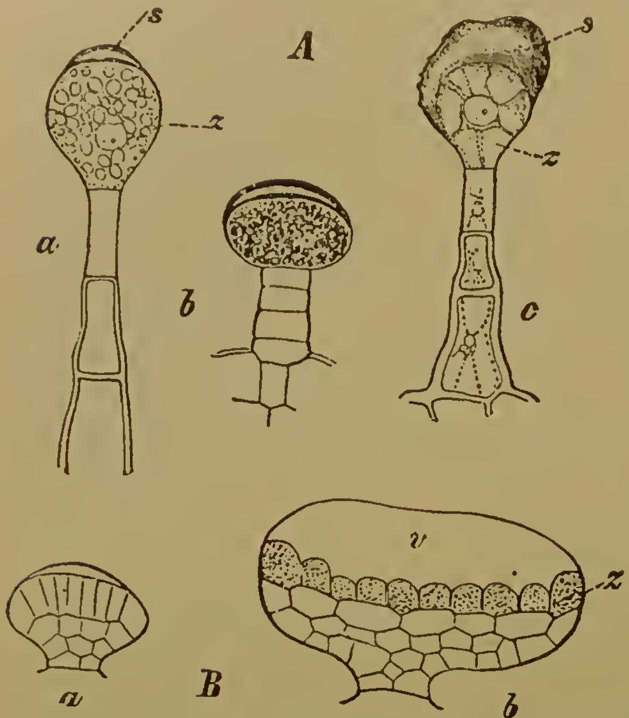

FIG. 93.—External glands: *A*, from the petiole of *Pelargonium zonale*; *B*, from the leaf of *Ribes nigrum.*

a. b. and *c*, Successive stages of development; *s*, secretion; *v*, receptacle for the secretion; *z*, secreting cells. (After Haberlandt.)

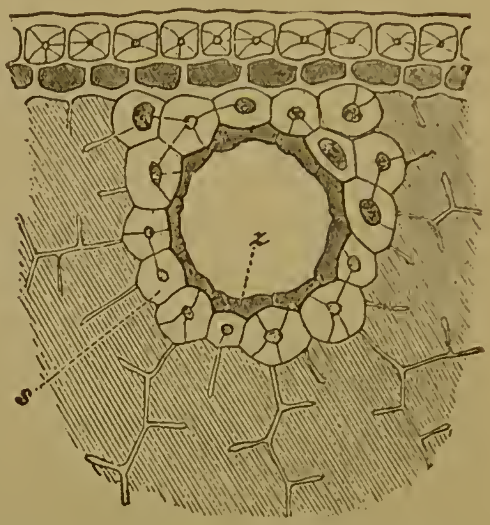

FIG. 94.—Resin-duct in the leaf of *Pinus silvestris.* (After Haberlandt.)

z, Secreting cells; *s*, protective sheath of the resin-duct.

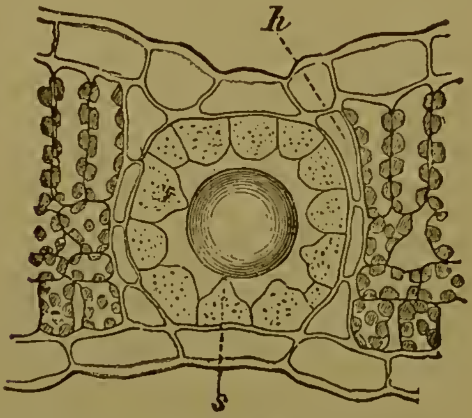

FIG. 95.—Oil-gland in the leaf of *Hypericum perforatum.* (After Haberlandt.)

h, Protective sheath; *s*, secreting cells.

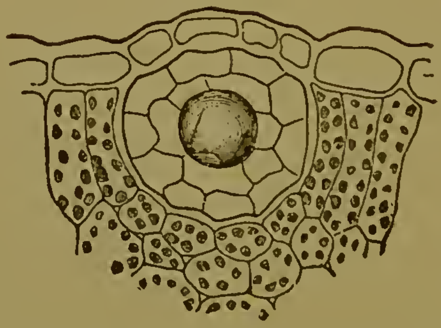

FIG. 96.—"Lysignian" oil-gland in the leaf of *Dictamnus albus.*

(After Haberlandt.)

PART III.

ORGANS AND SYSTEMS OF ORGANS.

When any given organ develops similar or dissimilar lateral organs we speak of the entire structure as an *organ-system*. In such a system there are members of different *order* and members of different *rank*. Members are of a different order when they have a different origin. The rank of different members is dependent upon a physiological inequality; for example, aerial members with green leaves and subterranean storage-tissue with scaly leaves are physiologically different.

We shall now treat (1) of the morphological and physiological differences of organs, (2) of the origin and arrangement of lateral organs and the causes of such arrangement, (3) of the difference in the development of the members of a system of similar organs (branching), which will finally lead us to the discussion of inflorescence. Although I have taken exception to NÄGELI and SCHWENDENER in the interpretation of fundamental principles, yet the general treatment of the subject matter in Part III is adapted from the works of the authors mentioned. As to the descriptive morphology, I shall adhere to RADLKOFER's method of treatment, and more especially to that of G. W. BISCHOFF.[1]

I. THE MORPHOLOGICAL AND PHYSIOLOGICAL RELATIONS OF ORGANS.

A. THE PRINCIPAL FORMS OF ORGANS.

In the course of this discussion we will find that it is necessary to add *physiological* properties to the fundamental *morpholog-*

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[1] Handbuch der botanischen Terminologie.

ical differences in order to bring out the characteristics of an organ.

In botany an organ is a cell-portion, a cell, or a cell-complex which is adapted to perform a definite life-function of the plant.

Morphological differences of organs do not always coincide with *physiological* differences. Organs that are equal in importance physiologically may differ very greatly morphologically, while organs differing physiologically may have similar morphological characters. Compare, for example, thorns and prickles, tendrils and climbing stems. Morphological definitions are dependent upon the history of development; physiological definitions upon function. Strictly speaking, morphology treats only of the *members* of a plant-body, while physiology treats of the *organs* (Sachs). We usually base the distinction of plant-organs upon morphological differences, while the modification or formation of organs is based upon physiology. The critical features of such a procedure will be discussed below.

1. The *thallome.* In the thallome there is no sharp differentiation between stem and normal leaf; this organ may resemble a stem or a leaf, or it may resemble both organs in different parts of the same plant. In its simplest form it is single-celled and not branched (examples: *Diatomaceæ*, *Desmidiaceæ*), or it may be branched, consisting either of a single cell or of a few cells. The lateral organs of the alga *Scytonema* are simply repetitions of the mother-organ, while in other algæ (*Caulerpa*, *Fucaceæ*, *Florideæ*) there is a marked distinction between the main plant-body and its lateral organs; the latter may represent leafy formations or root-like structures. The prothallium of ferns, a small green heart-shaped structure found on the soil in the forest or in flower-pots, greenhouses, etc., is a thallome. A thallome is therefore an independent vegetable structure devoid of organs, with perhaps the exception of trichomes.

The following organs are closely related to each other. The thallome may occur independently, but the trichome, caulome, phyllome, and root cannot occur independently.

2. The *trichome originates from the superficial* (*epidermal*) *cell-layer of various organs*, or more rarely from the epidermis and cells lying beneath the epidermis; so that we may distinguish between *epidermal trichomes* and *tissue-trichomes* (emergences). The spines on the fruit of the horse-chestnut, for example, are emer-

gences. The trichomes are not formed with any regularity or according to any systematic arrangement. Epidermal trichomes differ greatly in form (see Epidermal System, p. 53).

The two following organs

3. Caulome (stem-organ) and

4. Phyllome (leaf-organ) are so intimately related that they must be treated together. The *stem* (caulome) is really the central organ which bears leaves along the sides below the apex. The leaves are lateral organs on the apex and sides of the *stem and its branches* which are not irregularly formed here and there, but, in general, are developed *acropetally*, that is, from the base toward the apex (see Fig. 101). It is impossible to find any fundamental differences between the internal and external structure of stem and leaf. It is true leaves usually present an expanded surface, but there are likewise flat stems (*Cactaceæ*) and cylindrical leaves (*Coniferæ*).

5. The *root* is the organ whose cell-forming apex is covered by a protective tissue, the root-cap, and which *never* bears leaves. In contrast to trichomes and phyllomes, the root develops *endogenously*, so that it must force its way through some tissue before it can come to the surface. (The term "rhizome" does not have the same meaning as root, as we shall learn later.)

B. Modification of Organs.

(*a*) *Modifications of Stem and Root.*

Certain modifications of the caulome, due to its subterranean position, are of special physiological importance. Such caulome-organs are without foliage-leaves, or flowers. These modifications as well as a few root-forms will now be briefly discussed.

The following are the subterranean stem-modifications, of which there may be intermediate forms:

(*a*) The *rhizome* or root-stock—stem- and leaf-organ moderately developed.

(*b*) The *tuber*—stem enormously developed, leaves very small.

(*c*) The *bulb*—stem small, leaves very large.

At this point we shall introduce a biological classification of plants; that is, a classification derived from the life-processes of plants.

I. Monocarpous plants (*haplobioticæ*) bear fruit only once and then die. This occurs in one year in annual plants, in two years in biennial plants; in some after four or five years, as, for example, the *Agave americana*. (In our greenhouses this plant bears flowers only after about forty to sixty years.)

II. Polycarpous plants (*anabioticæ*) regularly form fruit each year on one and the same plant-body. Two means serve to maintain the plant-species: the periodical formation of seed, and the longevity or endurance of the plant. These plants may again be divided into two groups: 1, the aerial stem is woody and endures as such for a long time, as, for example, shrubs and trees, some of which are evergreen, while others drop their leaves; or 2, the stem is herbaceous and dies to the surface of the soil each year, but begins to grow again from a subterranean *perennial* stem. These are the *perennial* plants in the narrower sense, and in them occur the above-mentioned subterranean stem-modifications which serve as reservoirs for reserve food-materials (starch, water, albumen, etc.). Typical rhizomes occur among grasses and species of *Carex*; bulbs among *Liliaceæ*, tubers of *Solanum tuberosum* (potato). "Runners" may serve as asexual propagative organs; that is, *prostrate lateral branches* which have developed from subterranean buds may develop roots, stems, and leaves from the nodes.

Some of the aerial stem-modifications receive special names. The *culm* of grasses is a hollow stem with nodes at the attachment or insertion of the leaf and usually branching near the apex. The flower-stalk is nearly always free from leaves and terminates in a single flower or group of flowers. The culm of semi-grasses (*Cyperaceæ*) contains pith and is without nodes. There are tubers with *one* or *several* buds, depending upon the number of internodes represented. The potato has many buds situated in depressions and surrounded by scaly leaves. A peculiar case of a tuber with one bud is where the hypocotyledonous member, that is, the portion of the stem below the cotyledons, becomes thickened, as in the horse-radish.

The conception "tuber" is purely morphological, as is seen from the fact that orchid-tubers[1] are thickened secondary *roots*. In *Spiræa filipendula* secondary roots also become much enlarged.

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[1] The more precise morphology designates these as "tuberidia" instead of "tubers." These organs furnish the officinal mucilage of salep.

The main root, tap-root, *characterized as the direct elongation of the stem*, is often destroyed and its functional activity is taken up by the lateral roots. In plants developed from tubers and bulbs (many monocotyledonous plants) there is no main root.

Ordinary roots take up water and soluble substances contained in the soil (see Physiology of Tissues, II, B), and serve to attach the plant firmly to the soil. In warm moist climates many plants possess *aerial roots* whose physiological importance we have already learned to know. In certain cases (*Pandanus*, for example) these aerial roots may enter the soil and serve as organs of support; they may even form the only support for the stem. In other tropical plants the *branches* send out aerial roots which elongate and form supporting organs (mangrove trees; JOHOW).

(*b*) *Modifications of the Phyllome.*

The leaf-organ also presents various physiological forms or modifications. The observer soon learns to distinguish germ-leaves (cotyledons), cataphyllary (scaly) leaves, foliage-leaves, hypsophyllary leaves, and floral leaves. Before discussing these in particular we shall consider briefly the general morphology of the phyllome.

In the highest type the leaf may be divided into three morphological parts: leaf-sheath, petiole, and blade (*vagina*, *petiolus et lamina*) (Fig. 97).

If, however, only two of the parts mentioned were present, it would be wrong to speak of it as an undeveloped or imperfect leaf; there are, for example, leaves consisting only of the sheath-portion, as the bud-scales, bulb-scales, and rhizome leaves; these are nevertheless highly perfect. In those cases where one or the other of the parts mentioned is absent it is because it would be useless; this makes the part that is present so much more important from a physiological standpoint. In the discussion of the mechanical tissue-system we incidentally mentioned the mechanical function of the leaf-sheath. The *sheath* is the expanded basal portion at the base of the petiole or at the base of the blade; it encloses the stem. The stipules are special modifications of the leaf-sheath. Example: *Asperula odorata*; of the six or eight leaf-like structures arranged in a whorl two are true leaves

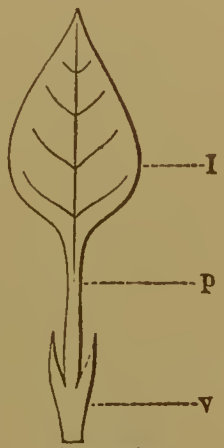

FIG. 97.

with axillary buds, the remaining two or four are stipules.[1] (Function of grass-ligules?)

The *petiole* is the stem-like support of the leaf-blade. If the petiole is absent, the leaf is said to be "sessile." Sometimes a leaf-portion resembling the petiole alone is developed, usually as a tendril. In some plants the petiole is flattened, as in the *phyllodes* of *Acacia*; these are not to be confounded with the *phylloclades* of *Ruscus*, for example, which are leaf-like stems and bear leaves themselves. In cross-section the petiole usually presents the appearance of a horse-shoe; such structural arrangement serves to increase the mechanical support.

The *blade* terminates the petiole of the sheath as the true leaf-expansion. In the assimilating foliage-leaves it is strongly developed, also in the petals of the corolla; the calyx is usually a modification of the sheath-portion. It is not intended to enter into an extended discussion of the morphology of the blade, though some such knowledge is necessary in order to understand the various modifications of the form of the blade.

Usually the blade is recognized as the leaf-surface or simply the leaf. It may be linear (about four times as long as broad), oval (about twice as long as broad), or elliptical (distinguished from the oval by the *angles* at apex and base). In regard to the base the leaf may be narrowed, rounded, cordate, auriculate or eared when the inner side of the lobe is rounded, hastate or halberd-shaped when the base is cut straight across, sagittate when the lobes are directed outward. The tip or apex of the leaf may be rounded, blunt, obtuse, mucronate, acuminate, truncate when it seems cut across, emarginate when there is a depression at the apex, obcordate when the depression is deep.

If the leaf-margin is not divided or cut, it is said to be entire; it is toothed when the projections at the margin point outward, serrate when the projections slant forward, crenate when the projections are rounded and the depressions pointed, sinuate when projections and depressions are both rounded. Usually the leaf-surface is even, sometimes repand, undulate, or wavy, especially toward the margin; or it may be variously folded, either longitudinally, transversely, or radially.

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[1] WARMING (POTTER), Handbook of Systematic Botany, 1895.

When the incisions are not limited to the margin, but extend more deeply, we distinguish:

1. Lobed leaves (*fol. lobatum*), when the incisions do not extend quite half-way to the midrib and the margins of the lobes are rounded.

2. Cleft leaves (*fol. fissum*), when the incisions do not extend quite half-way to the midrib and the lobes are pointed.

3. Parted leaves (*fol. partitum*), when the incisions extend more than half-way to the midrib.

4. Divided leaves (*fol. sectum*), when the incisions extend to the base or to the midrib.

All these forms, lobed, cleft, etc., are again separated into *palmately* and *pinnately* lobed, cleft, parted, and divided according to whether the direction of the incisions is toward the *base* of the blade or toward the *midrib.*

In the *compound* leaf the blade is divided into entirely separate parts; each part is called a leaflet (*foliolum*). It really seems as though the petiole were branched, each leaflet having a small petiole of its own by which it is attached to the common petiole. We may again have *palmately* and *pinnately* compound leaves. Sometimes the difference between a divided simple leaf and a compound leaf is not easily recognized. When we find the individual leaflets *jointed* or *articulated* to the common petiole in a way similar to that in which the latter is articulated with the stem, we may be certain that it is a compound leaf. The leaflets may be entire, dentate, serrate, etc.; or lobed, cleft, parted, etc.; thus we may have twice or thrice pinnately or palmately compound leaves. In the former case the leaflets are called *pinnæ*, in the latter *pinnulæ.*

Venation, that is, the arrangement and distribution of vascular bundles in the leaf, is intimately associated with the form of the leaf-blade. Most monocotyledons have *parallel-veined* leaves; most dicotyledons have *netted-veined* leaves. This venation may again be divided into *pinnately veined* and *palmately veined.*

We will now briefly consider the modifications of the leaf mentioned in the beginning of this section (*b*).

1. *Cotyledons* (embryonic leaves). Of these the monocotyledons have one, dicotyledons two, and gymnosperms few or many. They constitute the first leaf-like structures of the embryo, appearing almost without exception as entire lobes. With NÄGELI and others we may designate them as thallome lobes, since true leaves make

their appearance later. This fact, however, has no bearing on the theory of descent (evolution), as might be supposed.[1] There is no doubt that our most highly organized plants started from a single cell; of this *ontogeny* has given abundant proof. But to conclude from this that all plants in their successive generations are evolved *phylogenetically* is strange speculation. From arguments founded upon a natural basis we cannot accept such a hypothesis.

The most important facts in regard to the physiology of cotyledons have already been mentioned under assimilation.

2. *Cataphyllary leaves.* These leaves occur below the foliage-leaves; they not only occur near the base of the stem, but may be found near the base of branches. As already indicated, they are scaly and the blade-portion of the leaf predominates. The bud-scales, which serve to protect the bud during the winter months, are usually such cataphyllary leaves. As the name indicates, they are situated at the base of the future stem or branch; they, of course, are situated at the apex of the stem during the summer and autumn, that is, above the foliage-leaves of the *older generation.* The foliar structures of the above-mentioned subterranean stem-organs are cataphyllary leaves; for this reason the rhizome, the bulb, and the tuber are sometimes called "cataphyllary leaf-stems."

3. *Foliage-leaves.* The green leaves, usually recognized as leaves, are the typical organs of assimilation. Nearly all that has been stated in regard to the special morphology and physiology of leaves had reference to the typical assimilating leaves. Movements to place them in suitable positions with regard to sunlight, etc., will be discussed in a subsequent chapter.

4. *Hypsophyllary leaves.* The hypsophyllary leaves, also called

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[1] Nor can we accept HÄCKEL'S "biogenetic law," which states that phylogeny is repeated in ontogeny. For example, the embryo of the ferns (*Ceratopteris*) leaves its "thallome" state very early and forms the beginnings of a stem, root, and leaves, although "phylogenetically" it is certainly more closely related to the thalloid plants than to the phanerogamic embryos. If its thalloid nature is prominent in the idioplasm, why does it leave its thallome state earlier than does the embryo of phanerogams? Moreover, it follows (in opposition to NÄGELI) from the conceptions of stem, leaf, and thallome that a differentiation into stem and leaf must be preceded by a thalloid state, since leaf and stem are correlated terms. Nothing else seems *possible* than that a thalloid structure of one or more cells must precede the formation of stem and leaf. (Though many problems connected with the theory of descent are still unsolved, yet, in general, it is undeniable that the *phylogenetic* history of the individual, is so to speak, reflected in the *ontogenetic* development.—TRANS.)

bracts, are above the foliage-leaves and below the flowers. They are usually of a more simple structure than the true leaves; the petiole is wanting, *usually* the sheath and blade are *not* differentiated. They function as organs of protection for the young flower, as is well illustrated in the *bracts* of the genus *Allium* and in orchids, in the *involucre* of *Compositæ*, *glumes* of grasses, etc. The development and position of hypsophyllary leaves are based upon physiological and anatomical (teleological) requirements, and is not merely accidental. They occur most frequently in plants without a calyx, since they supplant the function of that organ.

5. *Floral leaves.* The peduncle terminates in the receptacle which bears the *floral leaves.* Their function is to aid in the processes of reproduction either *directly* or *indirectly.* By the term *flower* is understood a complex organ, a bud developed into sexual reproductive organs (Eichler). A flower is a modified branch. In the *inflorescence* we therefore have to do with a branching portion of a stem.

We shall consider the flower with its various so-called leaf-modifications, as calyx, corolla, stamens, and pistils, in Part IV (reproduction) in order to avoid needless repetition, especially as function is considered to be of prime importance.

In conclusion we shall add a few remarks on the coloring in the various leaf-modifications. The green color of foliage-leaves is of functional importance (assimilation); likewise the variegated coloring of floral leaves (fertilization by means of insects). The hypsophyllary leaves may be colored to perform the function of a foliage-leaf or of a floral leaf, or of both; likewise the calyx, though it is usually green. The cataphyllary leaves are rarely green; sometimes they are variously tinted, though the colors are usually not brilliant; often they are white.

Critical Observations on the Distinction of Organs.

As already stated, the term "organ" is a physiological conception. Yet it is customary to classify organs upon a *morphological* basis, especially according to the morphology of development. In such a procedure great care is necessary in order to avoid mistaken conclusions. If we consider the thallome, leaf, stem, root, and trichome as the five chief organs of plants, it will not be found difficult to add the *organs of reproduction* (since they originate in a manner similar to the trichomes or leaves (phyllome). An unwarranted procedure is to conclude that the reproductive organs are evolved from the vegetative organs, or, as it is usually expressed, "are derived phylogenetically." The advocates of the *theory of descent* either take its correctness for granted or seek to make it applicable to this or that case. We shall refrain from going beyond the conclusions based upon observed facts into the realm of phantasy and pure speculation. Also the classification of leaves as "leaf-forms" is not acceptable to those who wish to consider, for example, the cataphyllary leaves as phylogenetically derived from the foliage-leaves.[1] A few remarks on the "transition" of vegetative leaves into reproductive organs shall now be added.

In the first place it is evident that the stamens and foliage-leaves, morphologically considered, are both leaves, yet the difference between them is very great when we consider each as to its *function* in the mature state, since such a mode of treatment is appropriate here as well as it was in regard to the internal organs (tissue-systems). It is also clear that we cannot conceive of the origin of a stamen other than that it starts as a small wart-like cellular protuberance on the side of the stem. Finally, it is also clear that the young stamen will take such a course in its development as will lead to the formation of a pollen-bearing organ rather than of a foliage-leaf. The morphological conception of an organ is justifiable, but it must not be valued too highly.

Between the involucre and staminiferous flowers of the *Compositæ* occur the so-called neutral flowers, which to the observer seem to be formations of a double nature. It is, however, evident that in the development of stamens such intermediate states are not passed through; these neutral organs can hence not be looked upon as states of *transition*. Morphology based upon facts of development points out the great similarity between stamen and leaf, between most carpels with their ovules and divided or compound leaves; this similarity is further emphasized by the frequent occurrence of the apparent reversion of the floral leaf to a foliage-leaf. Every observer has no doubt witnessed such phenomena. But to conclude that such changes are evidence of the evolution of reproductive organs from purely vegetative leaves is wholly unwarranted; it has not been proven.

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[1] WESTERMAIER, Natur und Offenbarung, 1893.

It would be useless as well as nearly impossible to change our present terminology; for example, the expressions stamen-leaf, pistil-leaf, etc. It is, however, necessary to call attention to what I believe to be erroneous tendencies.

Palæontology cannot produce any evidence to show that phanerogams did not always possess vegetative as well as reproductive organs. There is no scientific basis for the assumption that our present phanerogams were preceded by ancestral forms with only vegetative organs.[1]

C. THE COMPLEX ORGAN: SHOOT.

The relation between caulome and phyllome leads to the following discussion. The leaf-bearing caulome is called a *shoot*, the young shoot is called a *bud*. The stem-portion between two successive leaves, or, in case more that one leaf occurs in the same horizontal plane, between two successive whorls of leaves, is called the *internode*. The *node* ("joint" or "knot") is that portion of the caulome on which the leaf is borne or inserted; it is often somewhat enlarged and differently colored. The entire habit of a plant depends in a high degree upon the length and thickness of the internodes. In the youngest stage the leaves are very closely crowded below the apex of the stem; the internodes are therefore very short, later many of them become much elongated. In general, it is found that the basal nodes remain short, followed by long nodes in the leaf-bearing region and again by short nodes near the apex; the phyllomes are correspondingly crowded near the base (basal rosette of many plants), higher up they are farther apart, then again more crowded near the apex. In the caulome of "unlimited" growth longer and shorter internodes frequently alternate; in such cases we find that the *cataphyllary* leaves are crowded; they indicate the boundary between two annual growths. Upon these follow foliage-leaves on elongated nodes, then again cataphyllary leaves on shortened nodes, etc.

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[1] These observations by the author may be of value in creating critical thought, but they cannot be considered as arguments against the theory of descent (evolution). To those transition-forms occurring among the *Compositæ* might be added numerous other examples; especially interesting is the case of *Nymphæa tuberosa*, in which the transition from green leaf through petal to perfect stamen is sometimes almost complete. It must, however, be borne in mind that such transitions are themselves the products of *phylogenesis*, and not of *ontogenesis*. To bring about permanent states of transition, as, for example, the conversion of a formative cell-group into a stamen rather than a leaf, requires at least millions of years, as the geologic record shows. In comparing a leaf with a stamen or with any other organ it must be remembered that *both* are the products of evolution, and that the *present* dissimilarities did not exist originally.

To my knowledge no scientist has ever denied that phanerogams as such did not always possess both vegetative and reproductive organs; they would not be phanerogams if they did not. The problem is to trace the evolution of the various organs, and to show how they are connected throughout the various groups of the vegetable kingdom.

The palæontologic record as far as it goes bears out the facts of evolution. Every scientist admits that the geologic record is of necessity broken, but even these gaps are becoming gradually less apparent.—TRANS.

Vertical shoots are, as a rule, structurally alike on all sides; horizontal branches and twigs, especially such as rest on the soil, show considerable difference of structure between the upper and lower sides. For example, it is found that the leaves on the horizontal stems of conifers occur along the sides to the right and left; in some mosses and in *Selaginella* there are structurally different *upper* and *lower* leaves. Upright shoots, therefore, have a *radial* structure, while horizontal organs have a *dorsiventral* structure (Sachs). These structural differences, which are dependent upon the influence of gravity and sunlight, also modify the habit of plants. The study of the stem and branches of the pine will make clear what has just been stated.

The bud is either *terminal* or *lateral;* in the latter case either *axillary*, or *adventitious* when its position is at *indefinite* points along the stem and not in the axil.

Vernation is the term applied to the position of leaves in the bud. The relative position of several leaves in the bud is called *æstivation.* Both conditions, compared with the mature state of the organs, show their peculiarities.

In regard to *vernation* the simplest case is where the leaf lies flat in the bud; the individual leaf may, however, be bent, folded, or rolled, either longitudinally or transversely.

Æstivation is *valvate* when the margins of the leaf-organs touch each other, or *imbricate* when the margins overlap; this latter may again be spiral or quincuncial (five-ranked), etc.

Before passing to the second chapter of this section we shall introduce a few statements in regard to *metamorphosis* and *correlation.*

D. METAMORPHOSIS AND CORRELATION.

It is highly essential that every one who devotes his attention to the different tendencies of our science should adhere to the purely botanical definition of metamorphosis. It would of course be a waste of time and energy to try to disprove such a thing as the occurrence of metamorphosis; however, it is necessary to dispel the erroneous conception that in metamorphosis there is a real transformation of one organ into another. Although we cannot follow the eminent morphologist GÖBEL in his explanation of organ metamorphosis[1] (I have stated my objections in Natur und Offenbarung, 1893), yet I agree with the author in his introductory statements that (1) there is a wide difference between true metamorphosis and the metamorphosis of GOETHE and A. BRAUN, and (2) in not a single instance have we been able to prove the phylogenetic origin of any leaf-formation due to real transformation. An important statement from so eminent an authority.

Cotyledons, cataphyllary leaves, foliage-leaves, and floral leaves show such great similarity in their early stages of development that one might well speak of them as the beginnings of members of the same morphological value. They are simply more or less extended cellular protuberances or warts upon lateral portions of the stem. However, in their subsequent development they are transformed into organs having widely different functions. Even what was originally the beginning of a leaf may not always develop into a leaf: it may develop into a prickle, tendril, or suctorial foot—organs which are no longer called leaves. Such a change in development is known in the vegetable kingdom as metamorphosis.

Based upon the above statements we may accept the following definition as given by SACHS in the year 1868:[2] Metamorphosis is the varied development of members of the same morphological value for the purpose of adapting them to definite functions.

One might incline to the view that since metamorphosis is identical with the *normal development* of the organs it is unnecessary to speak of them as "transformations." It must, however, be observed that the term metamorphosis implies that the originally equal morphological value is subsequently followed by a physiological dissimilarity. Occurrences in the vegetable kingdoms teach us that, for example, not all tendrils and thorny structures originate in like manner, that is, from rudiments known as foliar protuberances (tendrils of *Lathyrus* and spines of *Berberis*); some originate in the manner of branches (the tendrils of the grape, the thorns of *Rhamnus cathartica*). The conceptions "thorn" and "tendril" are therefore physiological, and not morphological. The second feature of metamorphosis is that morphologically unequal organs may be equal in value physiologically. Of this occurrence physiological anatomy knows so many examples that the entire phenomenon has come to be looked upon as a law of nature. The foregoing has shown us what metamorphosis in the botanical sense means. It is hoped that it has also made clear that it does *not* mean the transformation of *one organ* into *another*.[1]

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[1] Beiträge zur Morphologie und Physiologie des Blattes, Botanische Zeitung, 1880.

[2] Lehrbuch der Botanik; Vines' translation of the edition of 1874.

There is still another interesting condition to be mentioned: the correlation of the growth of organs. This is readily understood from the standpoint of teleology. One example will suffice to illustrate what is meant. If one cuts away the young shoots of a potato-plant, new lateral shoots will be formed which would otherwise have developed into tubers; that is, organs which were originally intended to remain underground and form storage-tissue for reserve material under certain conditions will form aerial organs developing green leaves having the function of assimilation. This phenomenon can readily be explained from the standpoint of *physiology*, but cannot be rationally explained from the causal-mechanics of organ-development, as SACHS is inclined to believe (see ref., p. 167).

II. ORIGIN AND POSITION OF LATERAL ORGANS, AND THE CAUSES FOR THEIR DEFINITIVE POSITION.

How is a system of organs formed? or, more specifically, *how* and *when* do new organs develop from those already existing? Upon *what* is the final position of the organ dependent?

These are the questions which shall interest us now. As is indicated, there is a difference in the origin of organs as well as in their succession. The position and arrangement of young organs are also different from their later position and arrangement (final or definitive position).

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[1] GOBEL'S metamorphosis of organs I have discussed elsewhere; also the subject of "correlation" as opposed to the views of SACHS (see citation above).

There are not less than seven different places of origin for the various organs of the more highly organized plants. They are as follows:

1. The *epidermis*. In it the *trichomes*, also the "emergences," with the aid of more deeply seated layers, have their origin.
2. The *apical portion* of the stem gives rise to branches.
3. The *terminal portion* of roots gives rise to secondary roots (dichotomy).
4. The *meristem* (formative tissue) of the stem-organ immediately below the apex gives rise to *leaves*.
5. The *tissue in the axils of leaves* gives rise to axillary shoots.[1]
6. The *cambium* and all other meristematic tissues within the epidermal layer of various organs, such as stem, leaf, and root, give rise to *adventitious* branches and roots.
7. The *pericambium* of the root gives rise to the normal root-branches.

Adventitious formations (6) and normal root-branches (7) originate *endogenously*, as opposed to the *exogenous* origin of organs mentioned under 1–5 inclusive.

From the various groups of cellular plants we shall select the following cases for discussion:

(*a*) Among many algæ branching of the thallome proceeds from the apical cell; well exemplified in *Florideæ* (Fig. 98, diagramatic).

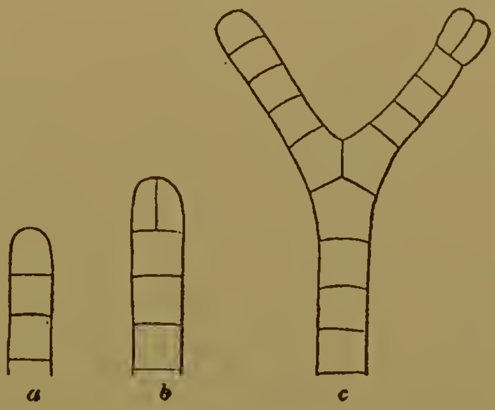

FIG. 98.

(*b*) In some algæ (*Cladophora*, *Characeæ*) the branches proceed from certain body-cells (Fig. 99). It may be that any or all body-cells can develop branches, or it may be that only certain special cells have that power.

(*c*) In mosses the conditions are quite different. At the apex of the stem of the moss there is, as a rule, a "two-edged" or a three-sided

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[1] Among angiosperms there is, as a rule, a young shoot for *each* leaf-axil; in gymnosperms this is not the rule (this may readily be observed in *Taxus* and other conifers).

pyramidal cell. In the latter case each segment may develop a leaf (see Fig. 100, diagramatic apical views). If each successive segment develops more strongly on one side, there will be produced

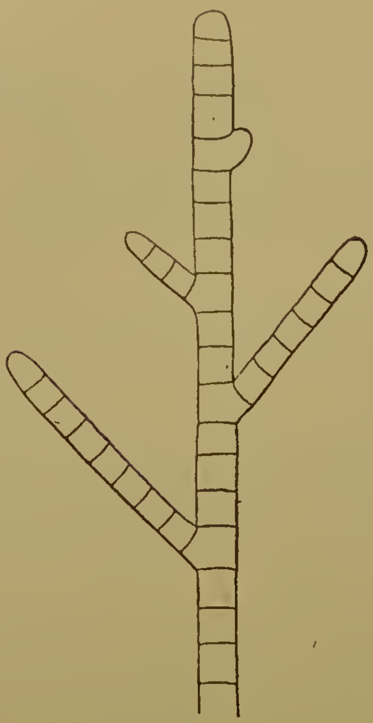

FIG. 99.

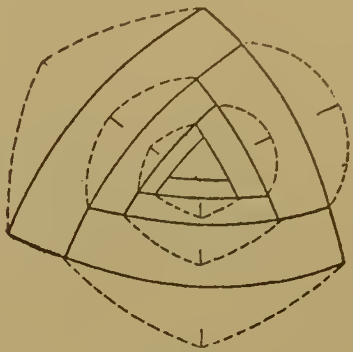

FIG. 100 *A*.

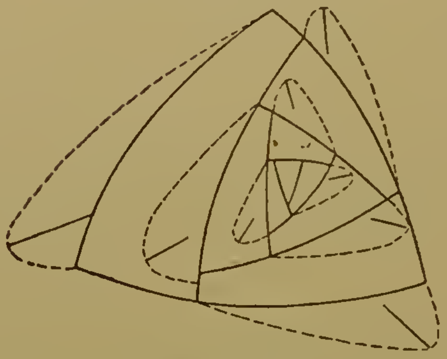

FIG. 100 *B*.

a spiral arrangement of the leaves (see Fig. 100 *B*, diagramatic apical view). In still other cases the halves of each segment (either side by side or above each other) may develop leaves or branches. (LEITGEB has studied the development of the mosses more particularly.)

In regard to the *position*, inclusive of the succession of development, of lateral organs we may distinguish the following cases:

I. Organs are *irregular* as to origin and position. Example: trichomes upon other organs.

II. The origin and position of organs may be in *longitudinal rows*, as is the case in secondary roots formed from the pericambium. The number of rows is dependent upon the number of primordial xylem-groups. The succession of their development is, as a rule, acropetally, therefore the youngest branch is always nearest the apex of the root. Longitudinal rows of lateral organs, such as secondary roots and leaves, also occur in creeping ("dorsiventral") organs.

III. Frequently organs originate and are arranged in *whorls*, as is seen in the case of leaves and branches. Two or more lateral organs may develop from the same horizontal plane of the mother-organ. Example: the two-leaved whorl of the *Labiatæ*, the three-leaved whorls of *Juniperus*.

IV. The organs are arranged in *spiral lines.* The so-called "spiral" position of leaves and branches will be more fully discussed in the following chapter.

A. SPIRAL ARRANGEMENT OF LEAVES. THEORIES OF PHYLLOTAXY.

A line continuing around the stem in the same direction and cutting the various lateral organs by the shortest path is called the *ground-spiral.*

This ground-spiral, according to more recent investigators, is not necessarily a genetic line (*genetic spiral*); that is, the leaves need not follow this line in the order of their development, although they may follow a spiral line subsequently. We shall base our statements upon the studies of SCHWENDENER.[1]

As indicated above, there are only a very few cases in which the *genetic line* corresponds to the *ground-spiral,* as in the leaf-forming segments of the apical cell of mosses (Fig. 100). In other plant-groups the spiral arrangement is different, even among those in which an apical cell cuts off segments in succession along a spiral line. It has been observed (Schwendener) that in the fern the course of the leaf-spiral is independent of the segmentation-spiral of the apical cell. Also in *Equisetum scirpoides* there seems to be no fixed relation between the leaf-*whorl* and the spirally produced segments of the apical cell. The flowers on the disk of *Helianthus* are evidently not always developed acropetally corresponding to the ground-spiral. The fact that apical cell-growth in the stem of dicotyledons is not well known in all cases adds to the difficulty of finding the relation of the leaf-spiral to the spiral of the apical cell-segments. Therefore it cannot be maintained that the spiral arrangement of the leaves in the ferns, dicotyledons and monocotyledons, corresponds to a definite spiral position of foliar protuberances near the apex of the stem. With Schwendener we must consider the following of importance in giving a clearer knowledge of the subject. The young lateral organs or leaf-beginnings, which appear as small protuberances, *touch* each other; they are bodies, and not mathematical points. *Each young organ touches at least two of the preceding organs*—so to speak rests upon them, similar to balls piled upon each other. We will not discuss the *causes* for the formation of an organ; they are unknown. It is evident that there must be a supply of food-substances in order that an organ may develop; why this supply takes place neither physiology nor morphology can explain (causal-mechanical explanation). We may, however, recognize the factors which determine the position of the developing lateral organs; these factors are (1) the relative size of the organs already existing and of the new organ, and (2) the direct contact of the previously formed and the new organ. The fact that the initial organs at the base of the stem are usually of constant size while the later initial organs become smaller in an acropetal direction is of morphological importance (Fig. 101).

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[1] Mechanische Theorie der Blattstellung, 1878. HOFMEISTER is recognized as having done the preliminary work in this line.

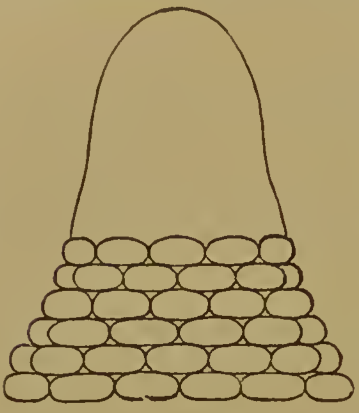
FIG. 101.—Sketch of the apical area of a slender stem showing the arrangement of the leaves.

Gradual *decrease in the size* of organs toward the apex, or *pressure* due to the growth in length and thickness of the stem, and the *growth* of organs themselves produce phenomena which may be expressed as follows: *Existing contact-lines disappear and new contact lines appear.*

Let us now continue the theoretical discussion of this subject.

The horizontal distance between two successive leaves, or in other words the angle which the median planes of the two leaves enclose, is known as their *divergence.* Usually when the leaf-divergence is given as $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, etc., it is found that the degrees corresponding to these fractions (120°, 144°, 135°, etc.) are only approximately correct.

In the divergence expressed by $\frac{1}{3}$ two leaves are separated by $\frac{360°}{3} = 120°$. A necessary result is (1) that the fourth leaf should be vertically above the first, since three divergences make the 360° of the circumference, and that (2) there are three vertical leaf-rows. In $\frac{2}{5}$ there are five divergences and two turns around the stem before we find two leaves in a vertical line. It follows that there must be five vertical rows, since the leaves 0 and 5, 1 and 6, 2 and 7, 3 and 8, etc., are vertical. In other words, the fraction indicating the angular divergence of leaves may be explained as follows:

The numerator indicates the number of turns about the stem, beginning with one leaf and terminating at the first leaf vertically above; the denominator indicates the number of vertical rows.

There are two methods for representing the leaf-divergence graphically: first, projection upon a horizontal plane, as in Fig. 102, which represents the divergence $\frac{2}{5}$. This method shows the vertical rows very clearly. The other method is that of representing it upon the plane of a cylinder rolled out flat. This brings out the spiral lines very beautifully, as shown in Fig. 103, which illustrates the divergence $\frac{3}{8}$.

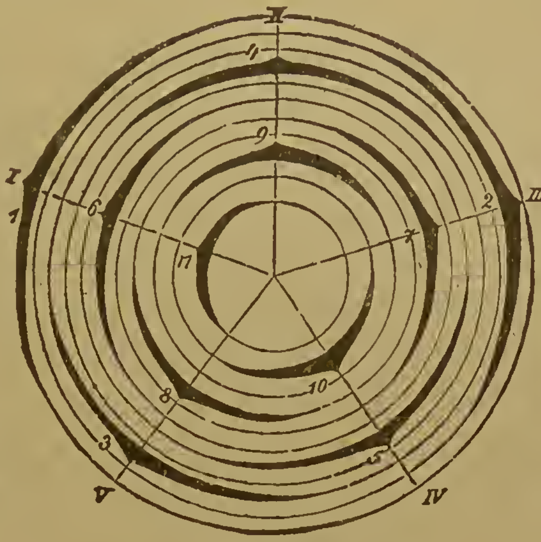

FIG. 102.
(After Sachs.)

The number of *vertical rows* also gives the number of leaves between two successive members of a series, as will be seen from a close inspection of the figures; for example, in Fig. 103 eight vertical rows are shown, hence the name eight-ranked.

Likewise the parallel diagonal lines cutting the leaf-organs also indicate the number of intervening leaves. For example, in the direction *ab* (Fig. 103) this number is five, in the direction *cd* it is three. These relations can be very easily studied in the cones of conifers. It must be borne in mind that this numerical relation

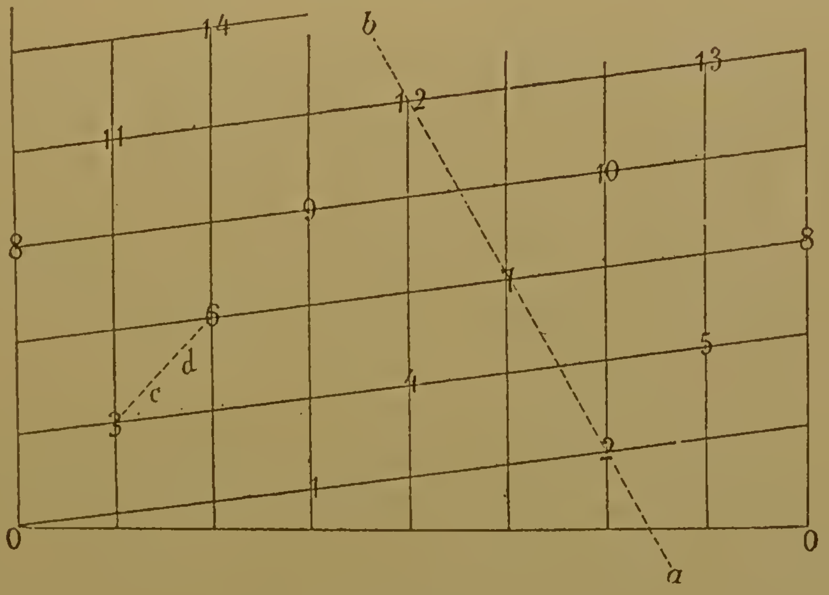

FIG. 103.

has no essential bearing upon the ground-spiral; they are simply "spiral lines" or "secondary spiral lines." Such *secondary spirals* become very distinct when the organs are closely crowded, as they are in pine-cones.

B. The Determination of a Divergence.

It is almost impossible to count the vertical rows as well as the turns about the stem when the angles of divergence are very small. In such a case it is customary to start from a given leaf (marked in some way) and to determine (1) the number of *distinct* diagonal rows, (2) the number of distinct rows crossing the former in an opposite direction, usually at nearly right angles. It is thus possible to number the organs upon a slip of paper, always starting from the marked leaf or starting-point. By drawing a line through two leaves having the same number the *horizontal* plane is found; then let fall a perpendicular cutting the horizontal and the leaf at the starting-point. The angular divergence may now be directly measured, or by the aid of the vertical line the number of turns about the stem may be counted, which will determine the fraction of divergence.

The fractions $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, $\frac{8}{21}$ (180°, 120°, 144°, 135°, etc.) give the (approximate) divergences of most frequent occurrence; the entire series is therefore called the "normal series." Further particulars will be given below.

By way of demonstrating what has been said, we will consider a few examples from nature. The cones of the red or the white pine show the divergence $\frac{8}{21}$ with great regularity; the series five and eight predominate in the secondary spirals. The given relation between the size of the stem and the size of the secondary organs is therefore quite constant, since the divergence in the stem and in the cone is the same.

It is also easy to determine the position of the first leaves on the axillary shoots of dicotyledons (shrubs). The pressure of the axillary leaf and the position of the primary axis tend to make the first two leaves develop to the *right* and *left*. The cause for the sinistrorse or dextrorse course of leaf-spirals is also mechanical; this is, however, not demonstrable without microscopic examinations (A. Weisse, of Schwendener's school).

C. The Mechanical Theory of Phyllotaxy and the Idealistic Conception of Nature.

Because of the important bearing of this subject upon the true idealistic and the so-called mechanical conception of nature I cannot refrain from commenting upon Schwendener's theory of phyllotaxy. By idealistic I do not mean anything fantastic and dreamy, but rather that clear and definite conception of the laws of nature as given by the Creator, and of matter as created by him; furthermore, that causality does not cease where causal-mechanics fail; that, moreover, the usual tendency of natural history or science to indicate this or that as something "given" points to the immaterial Giver as the highest Being and the Creator of all. It would be wrong to suppose that Schwendener's mechanical theory of phyllotaxy had, so to speak, destroyed the very foundation of the idealistic conception of phyllotaxy. Schwendener's mechanical principle of causality is far from satisfactory. The thoughtful investigator would naturally expect that the mechanical theory would trace complicated phenomena to simpler causes which must then be considered as granted or given.

The question why certain divergences occur most frequently was considered of great importance by the opponents of Schwendener's new theory. This question was proposed by C. de Candolle in the year 1881. The divergence fractions $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, etc., expressed in degrees approach the limiting value 137° 28′ 30″, which is the ratio of the golden section (*sectio aurea*) to the circumference of a circle. This is only true of the normal series; other series have different limiting values. The principal reason why the earlier advocates of the idealistic theory (C. Schimper and A. Braun) failed to substantiate their doctrine was because these authors treated the organs under consideration as mathematical points, and *not as bodies in actual contact.* To them the fractions of divergence constituted the part "given," while to us they are simply the necessary mechanical results of certain given relations. Although we reject the spiral theory of Schimper and Braun, we must not allow "number mysteries" to carry us too far, as they evidently did Schwendener, at least in his leading work (1878). In 1883[1] this author undertook the consideration of the question proposed by de Candolle.

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[1] Sitzungsberichte der Berl. Akademie.

His explanation of the phenomenon shall soon claim our attention. We, from our point of view, deduce from it that the finding of mechanical-causal relations does not imply that all idealistic conceptions of nature are thereby destroyed, but rather that it assists in exposing and making clear the great simple ideas. Schwendener has rightly named his theory of phyllotaxy the accessory theory ("Anschlusstheorie"). It is always necessary to assume a *basis*, or, so to speak, a frame, upon which or within which the arrangement of contiguous and variously superimposed organs, such as leaves and branches, must take place. This assumed basis for monocotyledons is the two-ranked arrangement of the single cotyledon and the succeeding leaves. See the copy of Schwendener's figure (Fig. 104).

In dicotyledons this "given" basis is the crossed position of the opposite leaf-pairs, an arrangement initiated by the two cotyledons. While the normal spiral of monocotyledons may be produced by other means than the acropetal decrease in size of the foliar beginnings, that is, by slow displacement due to longitudinal pressure, it is evident that such pressure, producing displacement of *equally large* organs in dicotyledons, would only convert the opposite whorl into a twisted whorl. But if one member of the leaf-pair is smaller, or if other irregularities appear in the crossing of the pairs, the above normal series 1, 2, 3, 5, 8, etc., will of necessity be developed provided there is a gradual decrease in the size of the organs in an acropetal direction.

According to Schwendener's explanation, it is again the *given basis* of the system, as well as the deviations from absolute regularity which necessarily work together to produce the spiral arrangement of organs in the dicotyledons.

Schwendener also studied coniferous seedlings which begin with a whorl of 3–8 cotyledons, and established the remarkable fact that, in spite of the unequal initial position of organs and irregular additions of subsequent organs, the final result is nearly always a normal spiral. These small deviations mentioned above, which are of normal occurrence, are the essential mechanical factors in the arrangement of lateral organs. TEITZ, a pupil of Schwendener, carried on a series of experiments which seemed to prove that longitudinal tensions proceeding from the vascular system of leaves and extending along the connected bundles of the stem determine the position of lateral organs. The causes leading to the position of leaves may therefore be stated as follows: The *given basis* of the system, the variations in size of the contiguous organs, and the tension-effects of the leaf-trace bundles.

The mechanical results of the morphological factors are the predominance of the normal series of divergences (limiting value:

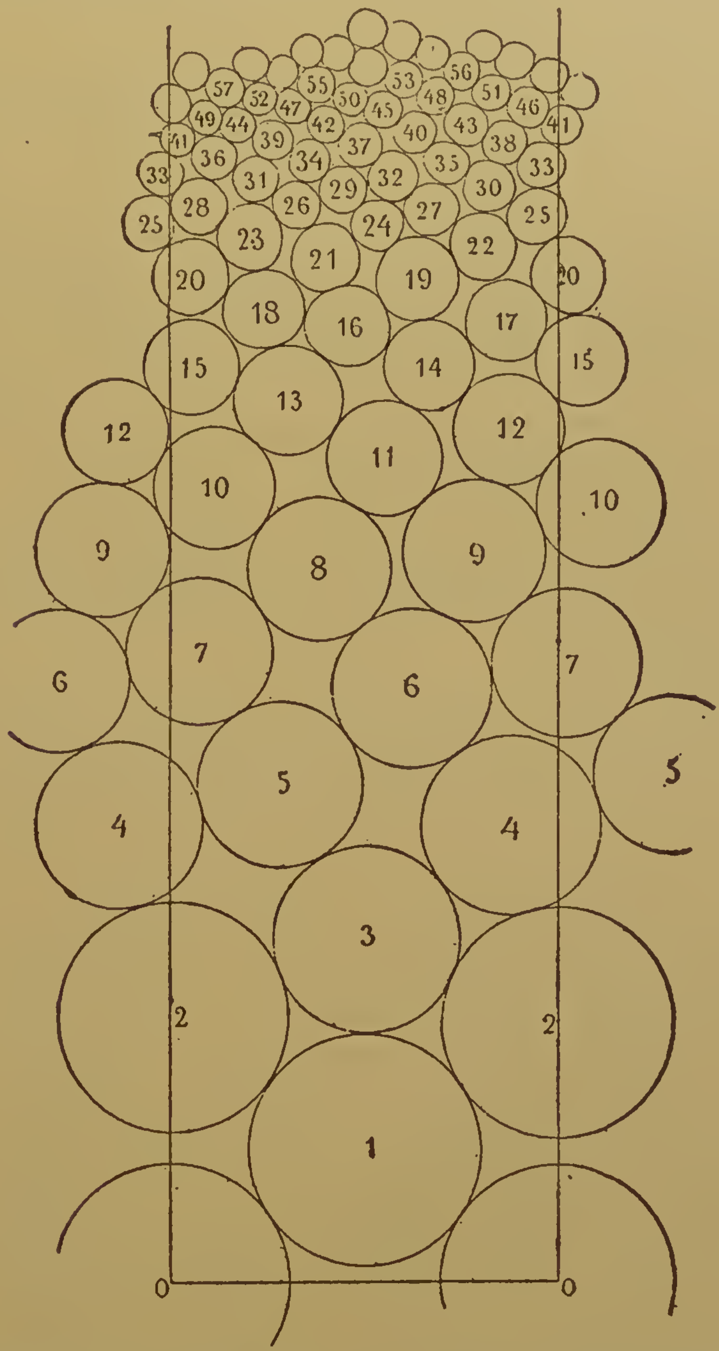
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FIG. 104.—Diagramatic representation of the transition from the alternating two-ranked arrangement to the spiral arrangement caused by the diminution in the size of the organs. (After Schwendener.)

relation of the golden section, extreme and mean proportion. (See above.) This phenomenon is, therefore, not purely morphological (Schimper, A. Braun, Bravais) but mechanically-morphological; for it represents mechanical results associated with almost constantly recurring morphological relations. With this statement I draw only one deduction from the investigations of Schwendener and his pupils. This is done in order to meet the superficial conclusions of some scientists, that the newer scientific teaching in regard to phyllotaxy does not leave a trace of the *idealistic* (in the author's sense) in the plant creation.

True and rational idealism is not at all disturbed by such materialism. The academic speech of du Bois-Reymond (Berlin, July 8, 1880) had only an oratorical value when he stated that Schwendener could pride himself as being one of those investigators who had aided in driving the "misty forms of vitalism" out of their "last hiding-place." The great fame of Schwendener is due to his achievements in the domain of pure scientific teleology. His authority as a botanist has been recognized for years, and will no doubt stand for many years to come.

In this problem of phyllotaxy repeated attempts have been made to give a teleological explanation,[1] but the real progress, which we owe to Schwendener, has been made with reference to another branch of our science.

The advance made evidently lies in that we can say: that mechanical relations—contact- and pressure-effects—are the *immediate* causes for the appearance of the divergences. However, there are many problems still unsolved. Why do certain plant-groups (monocotyledons, dicotyledons, gymnosperms) produce as a "basis" one cotyledon with alternating leaves, or two equally large, or three to eight nearly equally large cotyledons? Further, why does the gradual reduction in the size of the organs not appear regularly in plants where the divergence is approximately $\frac{2}{7}$? Why are vascular bundles (leaf-trace bundles) so united laterally that they must produce certain tensions at suitable periods? These and similar questions are still unanswered. We must admit that the chief merit of Schwendener's (in part also of Hofmeister's) discoveries lies in the fact that he has refuted the spiral theory, and in the introduction of mechanical factors into the domain of morphology. Schimper, Braun, as well as the Bravais and Naumann brothers looked upon lateral growth, especially the leaf-formations, as always following certain lines. There can be no genetic significance attached to the ground-spiral, nor to the secondary spirals or "parastichies," nor to the vertical rows or "orthostichies" (Naumann). We can only say that the position of organs is dependent upon the size, form, and the relative position of new organs and organs already formed. The activity of the leaf-forming apex of the stem is under the mechanical influence of organs already formed. The fact that many leaf-beginnings with wide divergences really correspond to the arrangement of the organs on the ground-spiral is not contradictory to what has been stated.

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[1] Depending upon adaptation to light and space.

III. DIFFERENCE IN THE POWER OF DEVELOPMENT OF THE MEMBERS OF EQUAL MORPHOLOGICAL VALUE. CLASSIFICATION OF ORGAN-SYSTEMS.

(*After* Nägeli *and* Schwendener.)

A system, as represented in Fig. 105, *A*, may be formed in different ways, and its difference as compared to other systems depends upon the mode of development. We will distinguish two forms of development, the *monopodial* and the *sympodial*. A monopodium is formed according to the plan shown in Fig. 105, *B*; a sympodium according to the plan shown in Fig. 105, *C*.

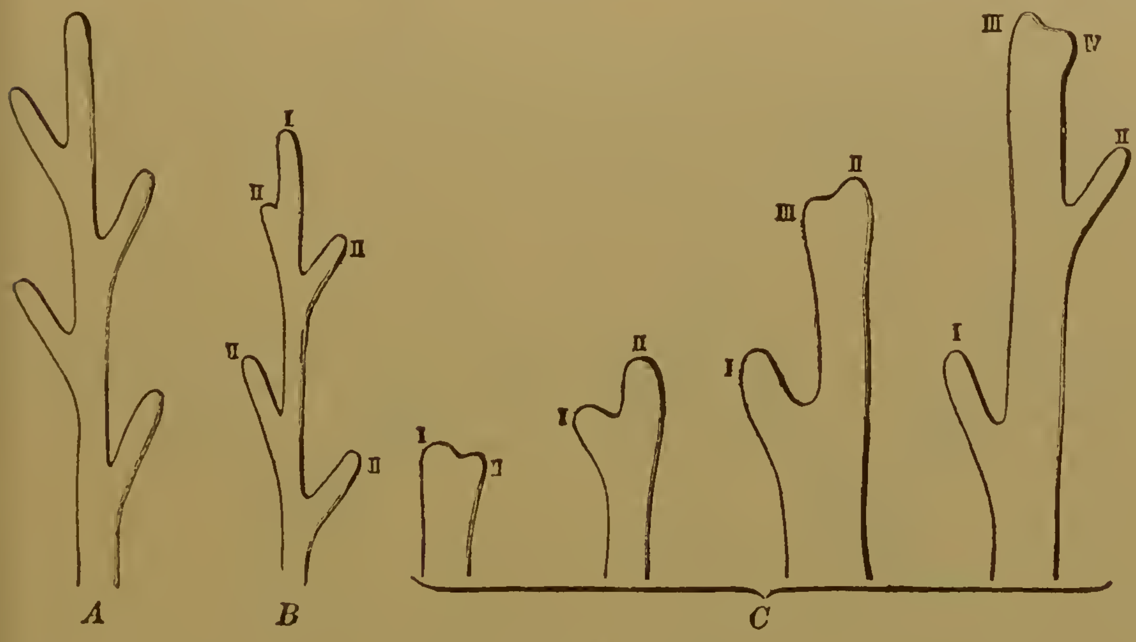

Fig. 105. (Diagramatic.)

In the monopodium (*B*) the primary axis represents the median line and grows most strongly, the lateral branches cease to grow early, and do not branch. In the sympodium (*C*) the upper part of the primary axis turns from the median line and develops a secondary branch or axis; the secondary axis takes the direction of growth of the primary axis, and finally divides again, forming an axis of the third order; this third axis bears the same relation to the second axis as the second axis bears to the first, and so on. This forms what is known as a "sympodium" or *pseudo-axis.* The rhizome of *Polygonatum multiflorum* is a good example (Fig. 106). The expression sympodium implies that the organ is composed of different *podia*, that is of shoots or branches of different orders.

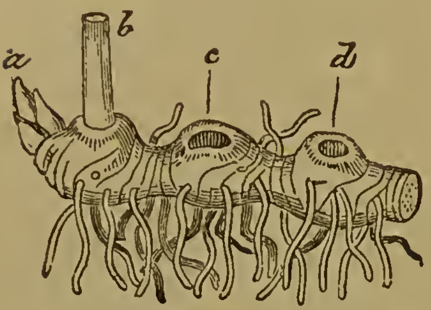

FIG. 106.—Rhizome of *Polygonatum multiflorum.*
a, Bud; *b*, basal portion of stem; *c* and *d*, stem-scars. (After Krass and Landois.)

Two organ-systems may be exactly alike in the beginning but may by wholly different in the mature state. This statement is contradictory to what was said at the beginning of this chapter. It can readily be supposed, and it is actually true that a spike and an umbel are alike at the beginning of their formation. The attempt to co-ordinate development and the mature state is liable to cause confusion. One must either trace the mature state back along the line of its development or *vice versa*, in order to have a correct understanding of the true conditions.

To trace the development of an organ-system is not always an easy task. An example, which incidentally introduces us to a very difficult chapter of morphology, will show that under certain conditions it is impossible to judge of the course of development from a study of the mature state. Very frequently there are deviations from the normal axillary branching. This I will attempt to explain

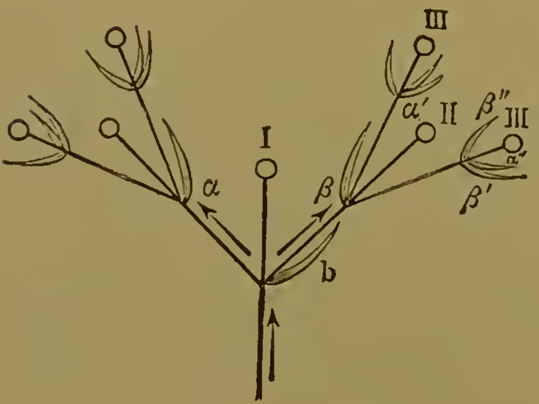

FIG. 107. (Diagramatic.)

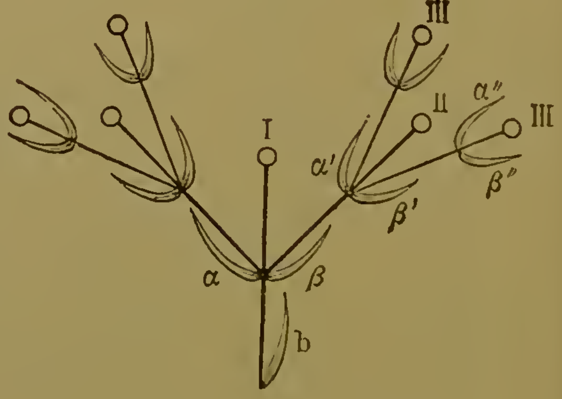

FIG. 108. (Diagramatic.)

with the aid of EICHLER's theoretical figures (107 and 108), used to illustrate the condition of things as they occur in *Datura Stramonium.* A normal development of bracts and axillary products would produce a structure similar to that shown in Fig. 108. The actual appearance, however, we find to be as shown in Fig. 107. Only in the youngest shoots (III) are the conditions normal, at least for the leaves α'' and β''. Leaf β', Fig. 107, although a bract of III, has been raised from its normal position, shown in Fig. 108. Every bract of the entire inflorescence thus shifts position as further shown by α and β; normally they should have the same position relatively to b, as α'' and β'' have to β'. The axes I, II, etc., terminate in flowers.

A. INFLORESCENCE.

Branching in the hypsophyllary region, the terminal branches bearing few or several flowers, occurs more frequently than a single floral axis with a single terminal flower. Such branching (with or

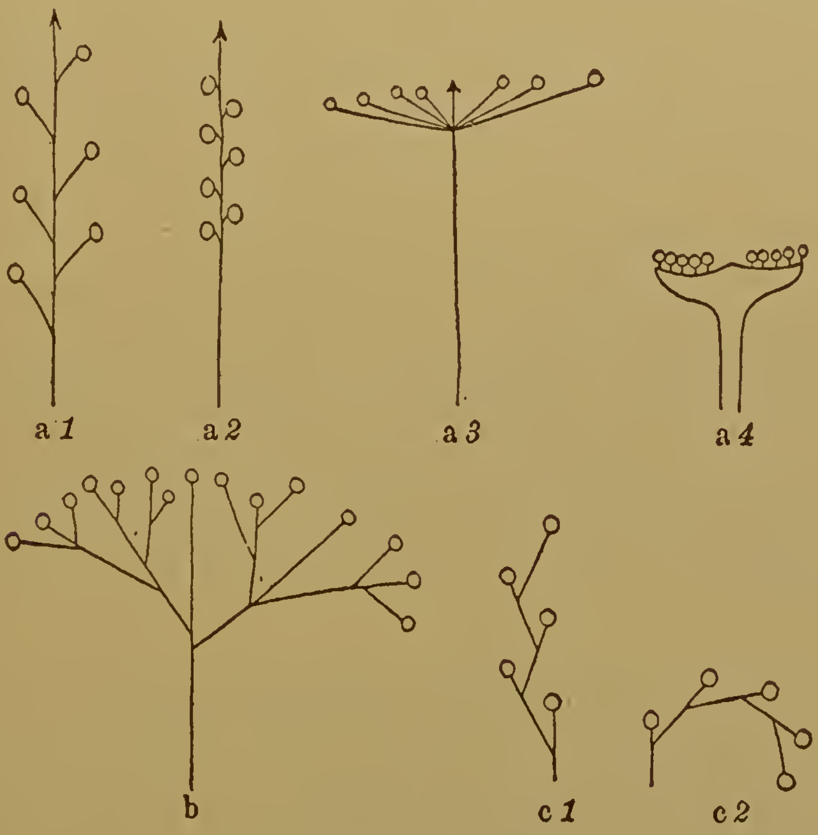

FIG. 109.

without hypsophyllary leaves), therefore, represents more than one flower, and is known as the *inflorescence.* We distinguish the following types of inflorescence, of which there may occur intermediate forms, usually classed with one or the other type.

(*a*) *Racemose Inflorescence.*

Primary and secondary axes exist. Primary axis does not terminate in a flower, secondary axes not branched, usually many, terminating in flowers.

1. *Raceme.* Primary axis long, secondary axes short.

2. *Spike.* Primary axis long. Secondary axes wanting or very short.

Subforms: *spadix*, primary axis fleshy; *catkin*, primary axis often pendulous and falling off after blossoming; *cone*, seminiferous scales woody.

3. *Umbel.* Primary axis short or compressed, secondary axes comparatively long.

4. *Head.* Primary axis short and cone-shaped or flattened, secondary axes wanting.

The following are the plants representing the types mentioned: 1, *Cruciferæ;* 2, *Plantago* (for the subforms: *Aroideæ*, *Salix*, *Pinus*); 3, *Umbelliferæ;* 4, *Compositæ.*

(*b*) *Paniculose Inflorescence.*

Axes all terminate in flowers and branch repeatedly; secondary axes of the first order predominate, decreasing in length and in the frequency of branching with the increase of the orders.

Panicle, as exemplified in *Alisma Plantago.*

Umbels with terminal flowers are at the same time paniculose and racemose.

(*c*) *Cicinnose Inflorescence.*

Repeated branching, each axis bearing only one lateral branch, which extends above the mother-branch.

To this inflorescence belong the *scorpioid* and *helicoid cymes* as well as the *dichasium.* In the two former the secondary axes are more or less at right angles to the primary axis, in the latter more or less parallel to the primary axis.

1. *Scorpioid cyme* (cicinnus, cyme, half cyme); secondary axes are arranged alternately to the right and left. Example: *Drosera.*

According to GÖBEL's investigations, the inflorescence of the *Borragineæ* cannot be included here. It is rather a dorsi-ventral raceme.

2. *Helicoid cyme* (bostrychoid cyme, bostryx); secondary axes all on the same side of the primary axis. Example: *Hypericum perforatum.*

3. *Dichasium.* This is really a slight deviation from the paniculose type in that the primary axis divides into two equally strong branches (*Silene*).

Different types of inflorescence may occur on the same plant, or the same type may be duplicated on the same stalk. In this way *complex inflorescences* are formed. *Umbelliferæ* have double umbels. Among *Gramineæ* small spikelets unite to form a panicle (oats), or again unite to form a spike.

B. RANK AND SUCCESSION OF SHOOTS.

Above the statement was made that there was a difference in the "rank" of various organs in a system as well as a difference in "order." While the orders are determined by the origin and development of members, the difference in rank of various members of a system depends upon physiological inequality. As a rule, each member develops secondary or lateral members of the same or next higher rank. The arrangement of branches in the inflorescence *absolutely necessary* to the development of flowers is usually different from those branchings not necessary, usually known as "accessory branches" (Bereicherungsprosse).

Case 1. The primary axis, or axis of the first order, bears an apical flower: "uniaxial" flowers, one rank. Example: *Helleborus niger.*

Case 2. A member of the second order is necessary to develop a flower: "biaxial" plants, two ranks. Example: *Paris quadrifolia* allows the axis of the first order to grow beneath the soil as a rhizome bearing cataphyllary leaves. In the axil of the third cataphyllary leaf there is formed a vertical member of the second order which terminates in a flower (A. BRAUN).

Case 3. Flowers are formed on members of the third order: "triaxial" flowers, three ranks. Example: *Lathyrus.* The members of the first order develop leafy shoots; the members of the second order develop floral spindles (axes of inflorescence); the members of the third order finally develop flowers.

The condition of affairs in the genus *Pinus* is especially noteworthy. *Long shoots* alternate with *short shoots.* The leaves (in clusters of two or more) occur on the short shoots; the long shoots bear scaly leaves from the axils of which the short shoots are developed.

PART IV.

REPRODUCTION.

INTRODUCTION.

In the process of reproduction *germs*, or in other words foundations for new individuals, are formed. These germs usually separate from the mother-plant when mature; sometimes they remain united to the mother-plant for a shorter or longer time, or even during the entire life-period. First case: The germs soon become separated; in this case they have special structural adaptations for the purposes of protection, distribution, etc., and, above all, special physiological properties. The most important reproductive germs belonging here have specific names: *seeds* (*phanerogams*), *spores* (*cryptogams*). Second case: The germs remain in organic union with the mother-plant during the entire life-period or only for a short time. (*a*) In mosses this union exists during the entire life-period of the plant. (*b*) In ferns the daughter-plant is set free by the gradual decay and disappearance of the mother-plant (prothallium). (*c*) In propagation by means of bulbs, corms, runners, stolons, etc., the daughter-plant is made independent by the gradual disappearance of that part which unites it to the mother-plant. Daughter- and mother-plant may then exist side by side independent of each other.

Reproduction, or the formation of new plant-individuals, is rarely limited to one method. In the same plant there are usually two or more methods of reproduction. The difference consists either (1) in that the germs are formed by different parts (organs) of the mother-plant; or (2) that one germ is formed sexually, the other by one or several of the various asexual methods; or (3) that the germs themselves and the plants proceeding therefrom are different.

We can now recognize two categories of phenomena which may both be observed on the same plant at different periods. When different methods of reproduction are united in the same plant-individual, we are not concerned with alternation of generation. If different methods of reproduction do not occur in the same individual, but alternate with the successive generations of a plant, we speak, in general, of *alternation of generation*. By alternation of generation we therefore mean the unequal behavior of the successive generations of the same plant with regard to the mode of reproduction. Concerning the first-mentioned phenomenon we will not have much to say; considerable, however, in regard to alternation of generation.

Let A and B represent different methods of reproduction (for example, sexual and asexual); they may be so distributed through the generations 1, 2, 3, 4, 5, 6, etc., that 1, 3, 5, etc., are the result of the method A; 2, 4, 6, etc., of the method B. Of very frequent occurrence is that form of alternation of generation in which method B is common to a series of successive generations, while method A occurs in only one generation; then another series of method B, etc. The following scheme will illustrate this:

$$\underbrace{\overbrace{\begin{array}{cccccccccccccc} 1, & 2, & 3, & 4\ldots & n, & n+1, & n+2, & n+3, & n+4, & n+5\ldots & n+m, & n+m+1, & n+m+2\ldots & \\ | & | & | & | & | & | & | & | & | & | & | & | & | & \\ B & B & B & B & B & A & B & B & B & B & B & A & B & B\ldots \end{array}}^{\textit{Series of Generations.}}}_{\textit{Methods of Reproduction.}}$$

In the case of alternation of generation the different forms of reproduction are equal in value in so far as they are necessary to the maintenance of the plant-species. The same may be said of all forms of reproduction. When there is no alternation of generation, but simply a combination of different methods of reproduction in the same individual, then these various methods are of unequal value, because, as a rule, one form of reproduction shows itself to be constant and more essential, and usually occurs at the conclusion of development, while the others (non-essential) make their appearance earlier. Example: a plant which finally produces seeds sexually, that is, from flowers, may in the course of its life-history be propagated from stolons, runners, corms, etc. Should these latter means of propagation fail to appear, the plant could, nevertheless, continue its existence.

At first glance the above general considerations and statements in regard to reproduction may not seem to have been very fortunately chosen. However, the student on entering more deeply into the phenomena coming under this category will soon recognize that the foregoing introductory statements, in which the author has followed Nägeli's concept of the subject, are sufficient to place the *essentials* of the endless variety of phenomena under a few comprehensive heads.

Germ-formation is very frequently sexual, as has already been stated. The male and female organs, which are essential in this form of reproduction, permit of the recognition of three different forms, dependent upon the relative position of these organs.

1. *Hermaphroditism:* male and female organs are in *immediate proximity*, for example, in phanerogams in the same flower; or on the same axis (among vascular cryptogams on the same prothallium).

2. *Monœcie:* male and female organs are on the same plant, but on separate axes; that is, the flowers are unisexual.

3. *Diœcie:* male and female organs are distributed upon different individuals of the same species.

A large number of flowers are hermaphroditic (perfect, bisexual), for example, our cereals, fruit-trees, legumes, the poppy, etc.; the birch, oak, hazelnut, and most conifers are monœcious; willows are diœcious. Monœcie and diœcie occurring together form *dicliny*.

Before entering upon the special discussion of the phenomena of reproduction it is important to introduce an observation on systematic botany. The essentials of our plant-system are taken from the domain of reproduction, and we may add that, as far as mosses, vascular cryptogams, gymnosperms, and angiosperms are concerned, it is more than probable that no other factors will supplant in importance those of reproduction. Algæ and fungi are separated from each other by the presence or absence of chlorophyll, and both are separated from the leafy mosses by the absence of leaf and stem; but within the algal and fungal groups themselves the factors of reproduction are utilized in establishing classes, orders, and genera. From this we may draw the conclusion that in a book like the one before us, in which taxonomy is not more fully treated, the special chapters on reproduction must also give a general concept of the systematic arrangement of plants.

I. REPRODUCTION AMONG CRYPOTGAMS.

We will speak first of the reproduction of cryptogams in general as compared with that of phanerogams. Generally the *seeds* of cryptogams are called *spores;* they usually consist of one or of a few cells and are mostly microscopic in size. In contradistinction thereto the seeds of phanerogams are larger and of a more complicated structure; they consist of several parts. The perfect phanerogamic embryo within the seed-coverings has essentially the structure of a bud.

Very frequently the spores of cryptogams are formed by asexual methods, and not as the result of fertilization. (Sachs[1] proposed the term conidia [‘‘gonidia’’] for all thallophyte-spores produced asexually; Eichler,[2] using the same term, applied it to the asexual motionless spores of fungi; while Warming wishes the term applied only to the asexual thallophyte-spores produced *exogenously.* It would no doubt be appropriate to follow the proposition of Sachs.[3]) The seeds of phanerogams are, however the direct product of fertilization.

There is also a series of cryptogamic spores which are the immediate product of two cells reacting upon each other. These spores are called *oospores* (egg-spores) when the two cells reacting upon each other are externally very different; *zygospores* (zygotes) when the uniting cells seem to be entirely or almost entirely alike: the latter process is called *conjugation.*

Most spores pass through a period of rest (resting-stage). With the maturation of the spores the plant for a time ceases to exist as far as that particular generation is concerned, as, for example, during the winter, or during periods of dryness. These spores ("resting-spores") usually develop at the next period of vegetation (spring, rainy season). On the other hand some spores develop soon after their maturation. They are usually endowed with a delicate membrane, as distinguished from the resting-spores, which have a more firm, usually colored, membrane. Such are the "swarm-spores," so called because they can move about in the water until they prepare themselves for germination. As soon as they are ready to develop they come to rest or fasten themselves in some suitable place. (Algæ and some fungi.) Sexual reproduction is not known to occur in all cryptogams; many investigators now agree with Brefeld that it does not occur among fungi.[1] Among the remaining cryptogamic groups—algæ (at least the great majority), mosses, and vascular cryptogams—sexual reproduction undoubtedly occurs. The *antherids* are the male sexual organs (among cryptogams); they contain the fertilizing elements, the *spermatozoids*. The *oogonidia* (egg-receptacle), or, when more complicated in structure, the *archegonia*, are the female sexual organs; they contain the egg-cell.

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[1] Compare Göbel's Grundzüge der Systematik.

[2] Syllabus, 1886.

[3] The term *spores* is, in general, also applicable to the reproductive organs of the so-called “higher” cryptogams—mosses and vascular cryptogams; they are also produced asexually.

The spermatozoids are either very minute oval cells or, among the more highly differentiated cryptogams, spiral threads. These threads are usually supplied with two *cilia* (organs of motion) at the thinner anterior end; the other end, which is usually thicker, contains plasm. The basal substance of spermatozoids (hence exclusive of cilia), according to more recent investigations (Schmitz, Strasburger, Zacharias), consists of "nuclein," that is, nuclear substance.

The oogonium contains the egg-cell. In its simplest form the oogonium consists only of a covering for the egg-cell. The egg-cell is frequently enclosed in a special organ known as the archegonium; in its form it usually resembles an Indian club of variable length. In the archegonia of mosses and vascular cryptogams one may recognize a shorter or longer "neck" and an enlarged base (venter) containing the egg-cell. The figures will assist in illustrating and explaining what has just been stated. They refer to algæ, mosses, and vascular cryptogams. Fig. 110 illustrates the

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[1] Perhaps also true of lichens; as already stated, Stahl's observations have not been verified.—Trans.

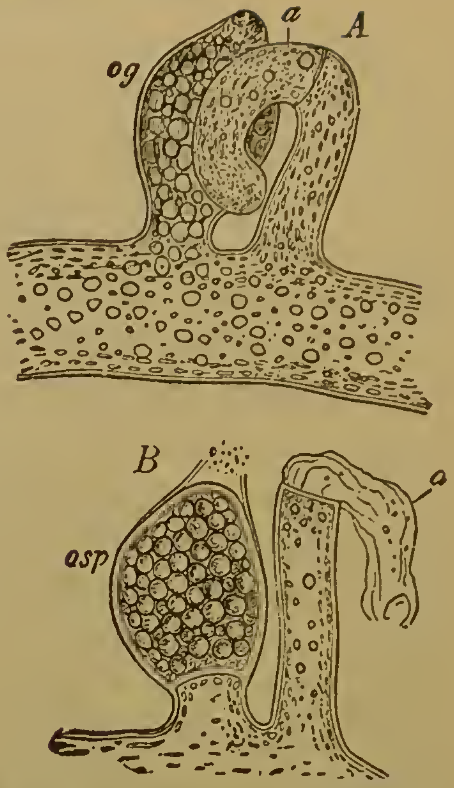

FIG. 111. — Sexual organs of *Vaucheria sessilis.*
og, Oogonium ; *a*, antheridium.
(After Sachs.)

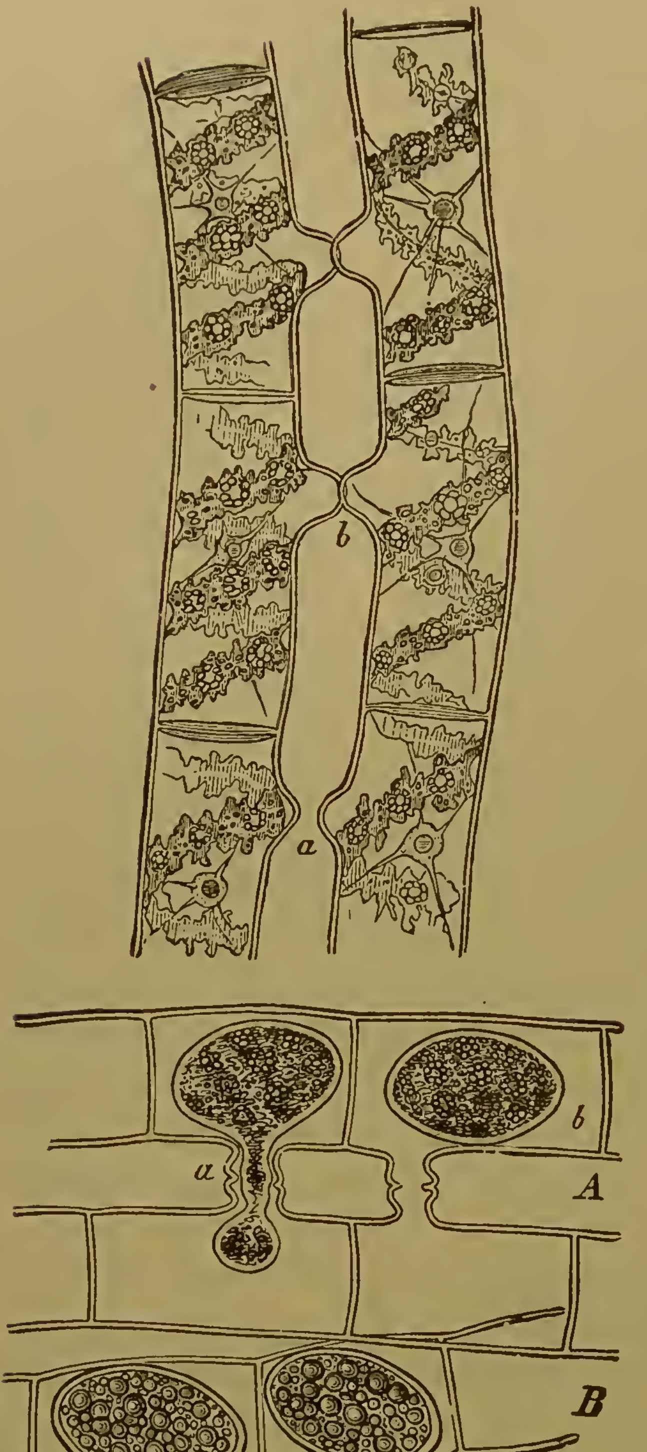

FIG. 110.—Various stages in the conjugation of *Spirogyra longata.*
(× 550.) (After Sachs.)

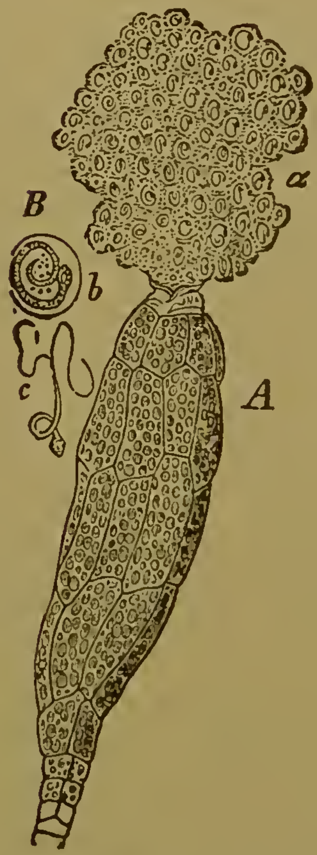

Fig. 112.—*A*, Rupturing antheridium of *Funaria hygrometrica* (moss); *B*, magnified spermatozoid in the mother-cell ; *c*, free spermatozoid of *Polytrichum.*
(After Sachs.)

processes of conjugation in *Spirogyra longata*; the upper portion of the figure shows two segments, the cell-walls of which begin to form projections at *a*; at *b* projections are in contact. Further progress is shown at *A*; at *B* the final stages are shown. Such conjugating cells are called "gametes." "Zoogametes" is the term applied to conjugating swarm-spores. Fertilization among *Vaucheria* differs very distinctly from that among *Spirogyra*; in the former the oogonium *og* (Fig. 111) is quite different from the antheridium *a*; *osp* in *B* is the *oospore* containing fat- or oil-globules.

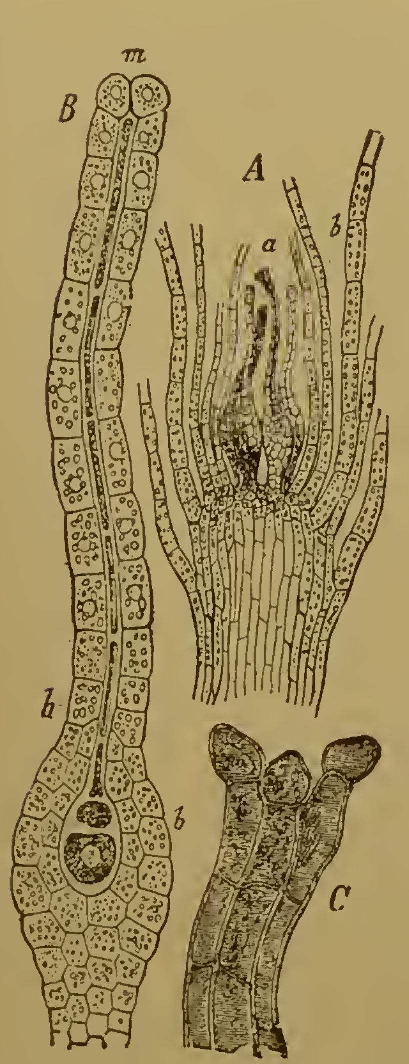

FIG. 113. — *Funaria hygrometrica.*

A, Archegonia (*a*) on the apex of the stem between the leaves (*b*); *B*, magnified archegonium (in glycerin): *b*, ventral portion with oosphere: *h*, neck of archegonium; *m*, mouth of archegonium, closed in *B*, open in *C* (after fertilization). (After Sachs.)

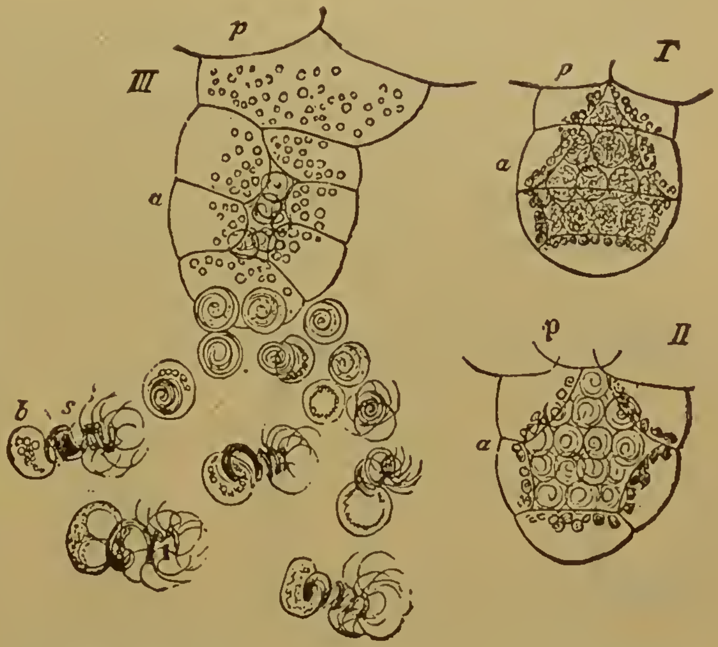

FIG. 114.—Various stages of the antheridial development of *Adiantum capillus* (I, II, III).

p, Prothallium; *a*, antheridium; *s*, spermatozoid with attached remnant of the mother-cell (*b*). (After Sachs.)

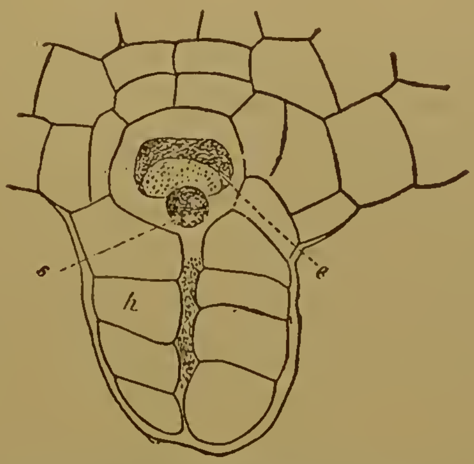

FIG. 115.—Longitudinal section of the archegonium of *Adiantum capillus*, before fertilization.

h, Neck; *s*, ventral canal-cell; *e*, oosphere. (After Sachs.)

A. Forms of Reproduction among Algæ.

Although the phenomena under discussion differ very greatly, we are enabled to see (among algæ) a well-marked relationship; there is, in general, an alternation of generation between sexual and asexual methods.

Among *Desmidiaceæ* (unicellular algæ) asexual reproduction by *division* alternates with reproduction by the conjugation of motionless gametes (see Fig. 19 in regard to reproduction by division).

Peculiar and interesting conditions are met with among the *Diatomaceæ*,[1] a group of unicellular yellowish-green algæ enclosed by a silicious membrane characterized by very beautiful and delicate striations and markings. A highly delicate organization associated with great reduction in size characterizes these truly marvellous creatures. (Ehrenberg, 1835. Otto Müller, Berlin, is at present well known as a specialist on diatoms.) Space will not permit a fuller discussion of the delicate structural markings; we can only mention them in so far as they are concerned with the processes of reproduction. The two parts of the silicious shell of the diatom fit each other as do the body and cover of a pasteboard box. For a series of generations reproduction is the result of simple division, hence asexual; then follows a special sexual generation (conjugation), which is again followed by division, and so on (see Figs. 116 and 117).

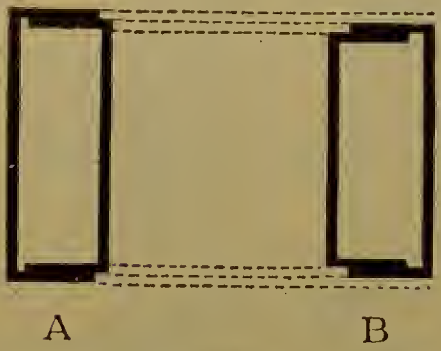

Fig. 116.—Diagramatic representation of two diatoms. Lateral view.

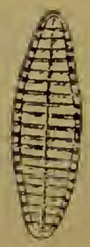

Fig. 117.—Top view of diatom. (Berthold and Landois)

The following statements are based upon direct observation. (1) Every division of a cell forming a diatom-individual (after cell-wall formation and separation of the two cells) gives rise to one (*A*) daughter-cell, equal in size to the mother-cell, and one (*B*) smaller daughter-cell. (2) There is no growth in length; as a result the smaller individuals must continually increase in number. The species would therefore be gradually reduced to such *small size* as to render existence impossible. Extinction due to decrease in size is avoided by two methods. The first, after certain pauses, fully restores the original size of the individual. This is accomplished as follows: *From time to time two small individuals unite with the escape and fusion of the cell-contents. This conjugation gives rise to an exceptionally large individual, sometimes two.* The second method is, so to speak, *corrective*, in that it *tends to retard the decrease in size.* OTTO MÜLLER[1] has discovered the following law of development: *The smaller of the two daughter-cells requires twice as long a period for the next division as the larger cell.* The large spores formed by conjugation are called *auxospores*, and are sometimes formed from a single individual (without conjugation).

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[1] Pfitzer made very important investigations of this group.

Protococcoideæ.—Either vegetative reproduction by division, or sexual reproduction by the union of swarming gametes which differ in external appearance.

Confervoideæ.—Asexual reproduction by means of swarm-spores; sexual reproduction by conjugation (*Ulothrix*). Antherids and oogonia are formed in some cases (*Oedogonium*, *Bulbochaetæ*). From PRINGSHEIM's classical investigations of the alga *Oedogonium* I select the following: The oospore formed during the previous vegetative season produces four swarm-spores which develop into new filamentous algæ. Swarm-spores are also formed from the vegetative algal threads. The oospore is the result of the fertilization of the egg-cell by means of the spermatozoids which enter through an opening in the covering of the oogonium. The spermatozoids are produced in two ways: either directly from the cells of an ordinary filament, or from a small few-celled male plant (*Zwergmännchen*). The latter is developed from an "androspore," a peculiar swarm-spore which, after liberation and swarming, comes to rest and, attaching itself in some suitable spot, develops a few small cells. From these cells the spermatozoids, which finally escape and fertilize the egg-cell, are formed.

Among *Characeæ* and *Vaucheriaceæ* there occurs a sexual propagation, besides sexual reproduction which is highly specialized in the former group. Among *Characeæ* propagation is accomplished by means of the vegetative protonema (Zweigvorkeime); in the latter group occasionally by means of swarm-spores (A. Braun, Pringsheim).

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[1] From the study of *Melosira arenaria*, Ber. d. Deutsch. Bot. Ges., I, 1883

Among *Fucoideæ* sexual reproduction is known in only a few cases. Much is yet to be discovered, though in some respects our knowledge concerning the comparative significance of the phenomena of reproduction is quite exact. The difference in the phenomena of reproduction in *Fucoideæ* and *Florideæ* may be readily explained from a teleological standpoint. The spermatozoids of *Fucoideæ* have cilia, therefore possess autonomous movement, while the fertilizing elements of *Florideæ* (red marine algæ) are without cilia, and hence motionless, and are called "spermatia" (σπέρμα, seed). In perfect harmony with such facts we find that the egg-cell of *Fucoideæ* is first set free and is endowed with autonomous movement, and may be reached by the equally free swimming spermatozoids. Among *Florideæ* fertilization is accomplished by the female organ ("carpogone") sending out a hair-like structure ("trichogyne") from the *fixed* egg-cell to which the spermatia become attached. *Florideæ* also reproduce asexually by means of "tetraspores"; these are formed by each mother-cell dividing into four parts (Bornet, Thuret, Pringsheim, and others).

B. Forms of Reproduction among Fungi.

The following is a brief summary of the chief forms of reproduction among the fungi. Asexual reproduction predominates. The asexual spores are produced either endogenously or exogenously. When exogenous, either basipetally or acropetally on the basidia or immediately on the mycelium. (The exogenous spores are sometimes called *conidia* in distinction to the endogenously produced *endospores*.)

We will first mention the two groups *Zygomycetes* and *Oomycetes* in which sexual reproduction usually occurs. As the names would indicate, we have conjugation with the formation of zygospores in the former group, and oospore-formation in the latter group. In the genus *Mucor* endospore-formation also occurs. ("mould" on bread, fruit, old damp clothing, leather, etc., belongs to *Mucor*.) Finally, we will mention Brefeld's chlamydospore-formation as an asexual mode of reproduction. By this is understood a "secondary morphological change" caused by some checking influence on the development of the sporangiophores, which then assume the function of spores. In a book of this kind it is well to adhere to facts obtained from actual observation, and not to enter into too many speculative considerations.

Among the *Oomycetes* there occurs reproduction by means of conidia and swarm-spores, besides the formation of oospores, mentioned above. As an example we may mention *Achlya lignicola* as one species of a group of fungi found upon dead flies and other insects, in water, etc. Fig. 118 (*A–E*) shows the oospore-formation. Fig. 119 shows the swarm-spore formation. The fungus *Phytophthora infestans*, which also belongs to this group, and which is so destructive to the potato-plant, has no sexual repro-

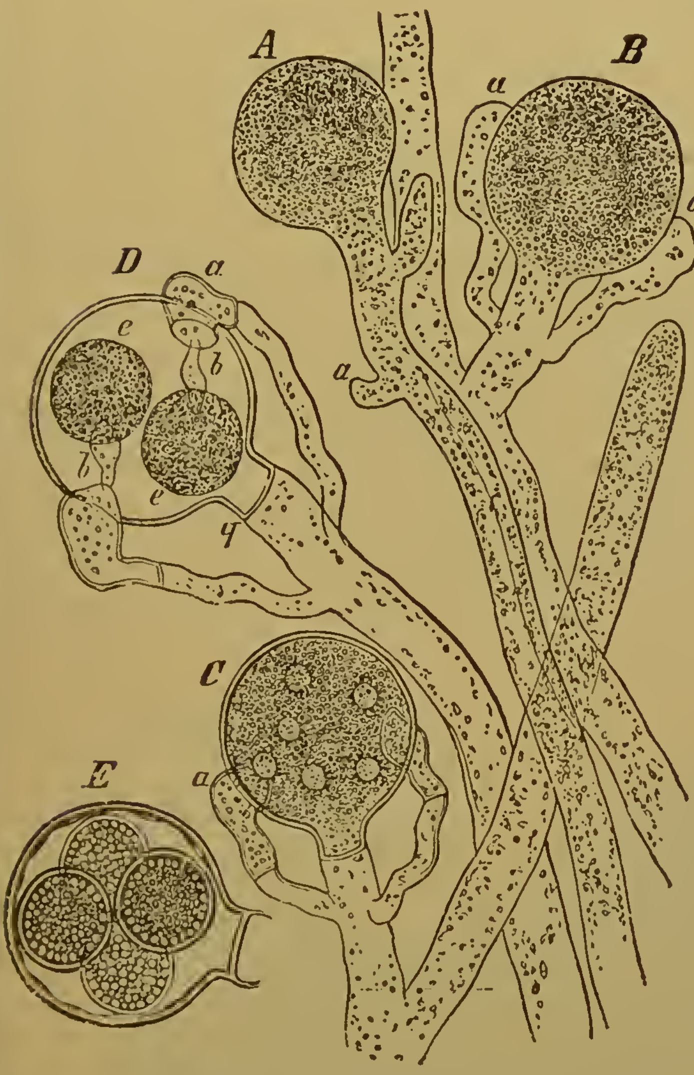

Fig. 118.—*Achlya lignicola.*
(After Sachs.)

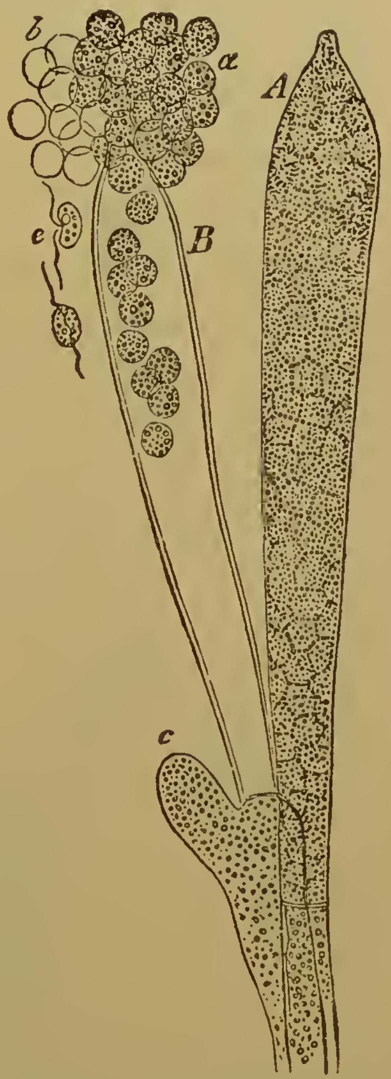

Fig. 119.—Formation of swarm-spores in *Achlya.*
(After Sachs.)

ductive organs, at least none have so far been observed. It has very minute characteristic conidial spores.

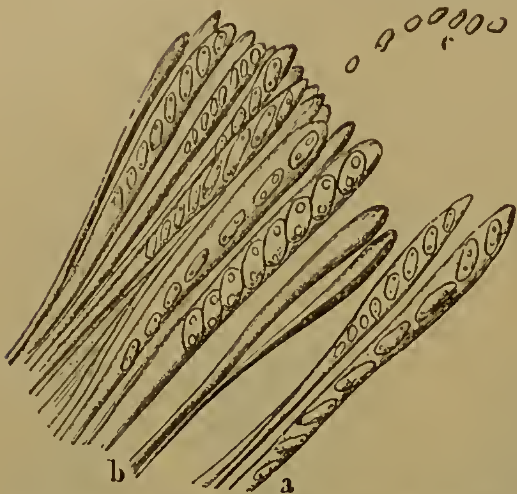

FIG. 120.—Asci, with spores, of *Peziza aurantia*.
(After Berthold and Landois.)

We shall now discuss the numerous fungi which have only asexual reproduction, namely, the *Ascomycetes*, *Basidiomycetes*, *Uredineæ*, and *Ustilagineæ*. The differences in reproduction as expressed in the names of the first two groups are illustrated in Figs. 120 and 121.

Within the two large groups *Ascomycetes* and *Basidiomycetes* there is in each a sub-group without a sporocarp or covering for the spore-bearing tissue; the remaining sub-groups have sporocarps. In regard to the two genera *Polyporus* and *Agaricus*, it is to be observed that they represent the essential differences between the *Agaricinei* and *Polyporei*; the lamellæ (gills) in the one and the pores in the other are simply different arrangements of the hyphal tissue especially adapted to give rise to spore-producing basidia. The following terms apply to the reproductive organs of many *Basidiomycetes*: *peridium*, *gleba*, and *capillitium*. The first is the covering which encloses the entire spore-bearing tissue of the *Gasteromycetes*. *Gleba* is the inner hyphal tissue enclosed by the peridium. This hyphal tissue contains pores or chambers; the walls of these pores are called *trama*, and are lined with

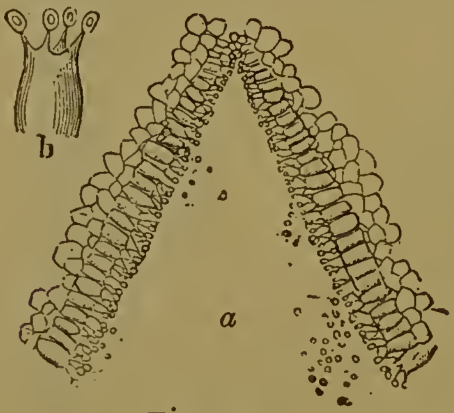

Fig. 121.

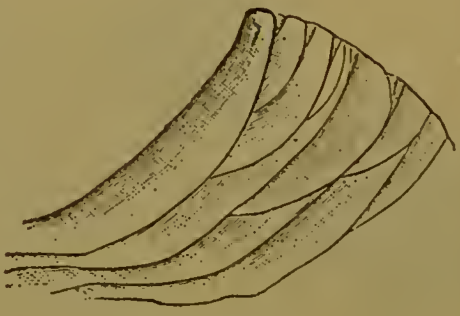

Fig. 122.

FIG. 121 and FIG. 122.—Gills (lamellæ) from the lower surface of a toad-stool. *a*, Moderately enlarged; *b*, basidium with four spores (highly magnified.) 122, Lamellæ. (After Berthold and Landois.)

spores. The spores are set free by the rupturing of the peridium, while the cells of the trama enter into dissolution, except certain cells which form a loose network of hyphal filaments, the *capillitium*.

The *Ustilagineæ* (blights) and *Uredineæ* (rusts) form either single terminal spores or chains of spores. Among the *Uredineæ* occurs a peculiar phenomenon called "heterœcie" (change of host) by its discoverer, DE BARY. Successive generations live upon different substrata, in this case upon different living plants (parasitic). Heterœcie is known in about fifty species of rusts. The names "blight" and "rust" already indicate that we are concerned with *plant-diseases*. We will first discuss the heterœcious rust-fungi, then the blight-fungi.

Puccinia graminis, the rust of our grasses, especially grains, is far more injurious than the blight-disease. Blight is limited to single plants of our cereals, while rust appears epidemically by its rapidly formed and germinating summer-spores. The methods of exterminating this plant-disease are as follows: 1. To destroy the "intermediate" host, which serves as a substratum for one generation: in *Puccinia straminis* the *Borragineæ*, and in *Puccinia graminis* the shrub *Berberis vulgaris* (see Fig. 123). 2. To destroy as many as possible of those plants which shelter the *teleutospores* during the winter months, that is, the remnants left in the

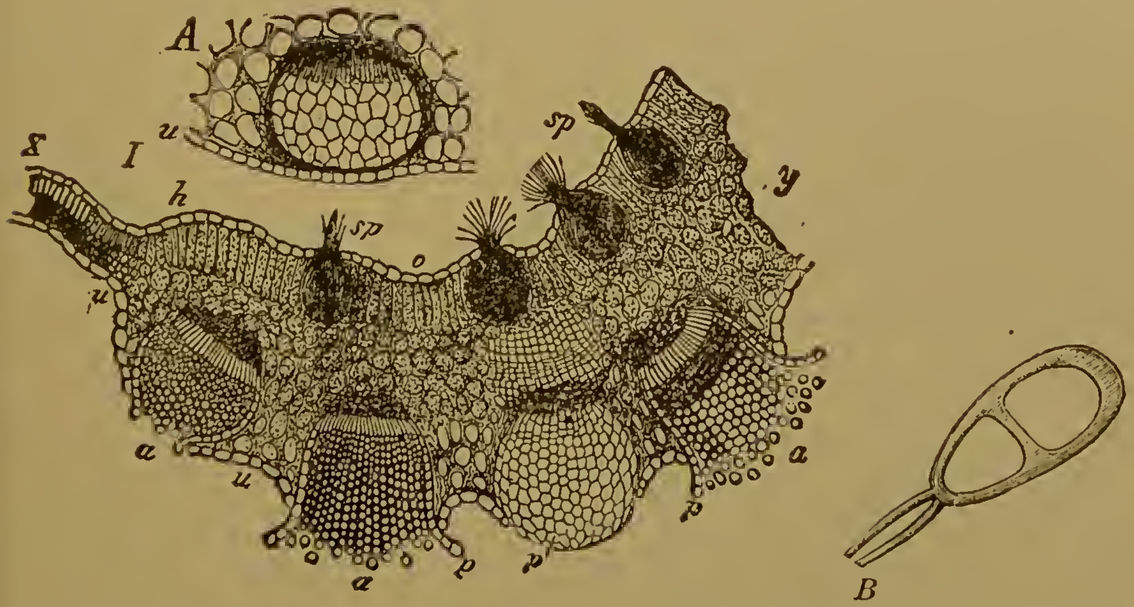

FIG. 123.—*A*, Young æcidium ; *Ia*, mature æcidia (*a*) on a leaf-section of *Berberis vulgaris* ; *B*, highly magnified teleutospore of *Puccinia graminis*. (After Sachs.)

grain-fields. 3. Grasses growing wild in the grain-fields (example: *Triticum repens*) often serve as hosts to the fungus. These must also be destroyed.

The course of development in *Puccinia graminis* is as follows: (*a*) The fungus lives upon the leaves of *Berberis vulgaris* during the spring and produces æcidiospores (Fig. 123, *Ia*, *A*), which are carried to the wheat- or oat-plants by the wind; (*b*) germination and growth begin at once and end with the formation of uredospores, which may be carried to other plants and also develop. (The spermagonia and spermatia shown in Fig. 123, *sp*, are little understood. Formerly they were supposed to be male sexual organs.[1]) The earlier the fungus attacks the plants the more injurious are the effects. Sometimes all the leaves are infected, even the glumes. Toward the close of the vegetative period (*c*) teleutospores are formed, which remain at rest during the winter months and begin to germinate in the early spring. From them grows (*d*) a *promycelium* with *sporidia*. The sporidia develop upon suitable hosts (in this case upon the leaves of *Berberis*) and again form æcidiospores, thus forming the beginning of a new cycle of development.

Tilletia Caries causes the smut of wheat; various species of *Ustilago* cause the blight of different grasses, especially of oats, barley, and wheat. (To prevent the occurrence of both of these fungi it is necessary to soak the seed to be sown in a ½ per cent solution of sulphate of copper for about twelve or fourteen hours and then to sow the seed during dry weather.) In this disease spore-formation takes place in the *ovarium* with destruction of the *ovulum*, while the assimilating organs (leaves and stems) are not attacked, as in rust-diseases. The spores adhere to the outside of the seed; hence it is advisable to soak it in a copper-sulphate solution of sufficient strength to destroy the spores without destroying the germinating powers of the seed. The group of fungi to which *Tilletia* belongs develops conidia upon basidia which are peculiar in that they arrange themselves in the form of an H before developing into a mycelium, which again produces rust-spores.

In conclusion we will mention reproduction in a fungus from the group of *Ascomycetes*, namely, *Clavipes purpurea*, usually known as *sclerotium* in its resting stage. This plant has potent medicinal properties. In its general outline the sclerotium takes on the form of the rye-grain which it attacks; it is usually larger and somewhat curved. It consists of a closely woven network of hyphal filaments (mycelium) forming a firm semi-cortical structure, brown externally and white internally. Infection takes place as follows: The surface of the young rye-ovary is covered by a mycelial network (honey-dew) which also penetrates the interior. Conidia are formed on the exterior. This conidia-forming network was formerly known as *Sphacelium* and was supposed to be a distinct fungus. Near the base of this structure the mycelium of the sclerotium begins to form; this develops rapidly and in its mature state bears the remnants of the sphacelium and the rye-ovary on its apex. The sclerotium is a "pseudo-parenchyma," that is, the hyphæ of the fungus are so closely interwoven that they resemble a parenchymatous tissue. (Such pseudo-parenchymatous tissues are also met with among lichens.) The conidia, which are formed when the rye is in blossom, constitute the first means of propagation and spreading from seed to seed. The sclerotium, which lies dormant during the winter months, develops elongated spores in the spring. These spores (ascospores) constitute the second form of reproductive cells of this fungus. Under favorable conditions the ascospores may develop in the fall, but the sclerotium is specially adapted to withstand the vicissitudes of the winter season, so that its spores may develop into the sphacelium-stage during the following spring. Preventative measures: Since this fungus is in great demand by druggists (even imported from America), it will pay doubly to collect the sclerotia before the grain ripens.[1] In the second place non-infected seed-grain must be selected. It is also well to destroy such grasses as *Lolium perenne*, which frequently spreads the fungous disease.

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[1] See foot-notes on pp. 189 and 200 in reference to spermagonia of lichens.—TRANS.

Reproduction among lichens[2] is the same as in that group of fungi which constitutes the fungal symbiont in the lichen-structure. In the great majority of lichens the fungal portion is derived from the *Ascomycetes*, a few genera from the *Basidiomycetes*. They also reproduce by means of vegetative organs, the *soredia*, which are formed in great numbers upon the lichen-thallus and are carried long distances by the wind. *These soredia contain both constituents of the lichen-body, alga and fungus.* For certain *Ascolichenes* STAHL has very probably demonstrated the existence of sexual reproduction.[1]

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[1] It might be mentioned that such a procedure would scarcely be successful in the large grain-fields of America.—TRANS.

[2] Their structure was briefly discussed under Symbiosis.

II. A COMPARATIVE STUDY OF REPRODUCTION AND ALTERNATION OF GENERATION IN MOSSES, VASCULAR CRYPTOGAMS, AND PHANEROGAMS.

Comparative morphology shows certain *analogies* occurring in the course of development in the above-named great groups of plants. Considering this fact from the standpoint of the doctrine of creation does not reveal anything surprising. It rather confirms and elucidates the workings of that uniform idea which called into life and controlled the great series of vegetable organisms. The intellectual work which disclosed these analogies appears the more gigantic since the resemblances are often indistinct, or on the other hand the actual differences between the various groups to be compared are often very abrupt. HOFMEISTER must be credited with first having revealed these analogies. Human intellect has received the ability to comprehend the Creative Idea within a certain limit. The fact that the stated differences or boundary-lines between the great divisions of plants are intellectual, that is, can only be bridged over by processes of thought, decides in favor of our conception of the subject. Concrete connecting links as they are supposed to exist by the believers in natural descent cannot be demonstrated. Although our conception of this subject-matter differs from that of the prevailing tendency in the wider scientific circles, yet we maintain that our process of reasoning is founded upon a purely scientific basis. The existence of points of similarity notwithstanding evident contrasts indicates the ruling of a uniform idea; only the speculative fantasy of the theory of descent finds it necessary to construct concrete connecting links between these existing contrasts.

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[1] Recently STURGIS has apparently verified STAHL's observations. In some instances the supposed male sexual organs (spermatia of Stahl) are very likely spores of a *parasitic fungus* (spermagone of Stahl) *living upon the lichen.* Further investigation is necessary.

(It should be noted also that the most recent writers on lichenology (REINKE) consider lichens as *autonomous*, having a *phylogeny* of their own, and should therefore be considered as a *distinct class.*—TRANS.)

In regard to the differences just mentioned, the following shall now be mentioned, although the beginner will only comprehend the subject fully from what will be stated later.

1. No pollen-grain of a phanerogamic plant is capable of producing motile spermatozoids, while on the other hand no microspore of a vascular cryptogam can develop a pollen-tube.

2. By comparing the phanerogams with viviparous animals, as Sachs has done, we find that the contrast between vascular cryptogams and phanerogams is too great to enable us to compare the vascular cryptogams with oviparous animals. This fact Sachs himself emphasized.[1]

3. Although the antheridia and archegonia of vascular cryptogams and leafy mosses resemble each other, it is evident that the relative behavior of sexual and asexual generation is materially different. Among mosses the leafy plant develops from spores produced asexually, while among vascular cryptogams the plant proper is the product of the fertilized egg-cell. NÄGELI, the shrewdest and most zealous supporter of the theory of descent, supposes that the present phanerogams were derived from former, now extinct, vascular cryptogams, and these from moss-like plants.[2]

We shall now enter more fully into the particulars of this comparative study. Let us suppose the entire development of a plant, beginning with a reproductive cell and terminating with a cell of equal value, to be represented upon a circle, as is shown in the accompanying diagramatic sketch (Fig. 124, 1, 2). This shows the relation between a moss and a fern. 1 Represents the moss and 2 the fern; *G* the sexual generation and *U* the asexual genera-

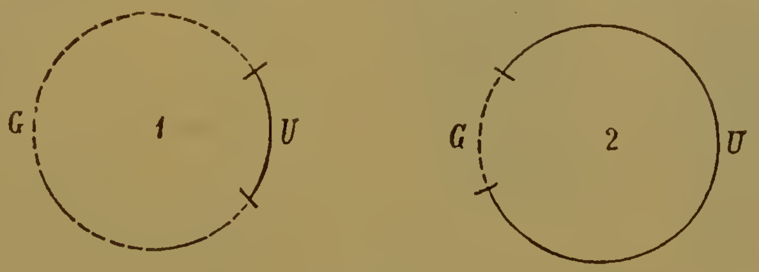

FIG. 124.

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[1] Vorlesungen, p. 922.

[2] Mech.-phys. Theorie der Abstammungslehre, p. 472.

tion. Among mosses the sexual generation (*G*) is *prominent*, it forms the independent green plant; the asexual generation (*U*), which forms asexual spores, does not even have an independent existence; it exists, so to speak, as a parasite upon the leafy moss-plant forming the *sporogonium* (moss-capsule, spore-fruit). Among vascular cryptogams the large leafy plant constitutes the asexual generation, while the minute green, short-lived structure called the *prothallium*, represents the sexual generation upon which the archegonia and antheridia are formed.

In regard to the structure of the sporangium of mosses, I will state that the capsule of most liverworts contains spores in the internal axial space, while in the leafy mosses the spore-bearing area takes a more peripheral position, that is, between the sterile central column (columella) and the wall of the capsule. For the present we will omit further particulars. Figs. 125 I and 125 II, as

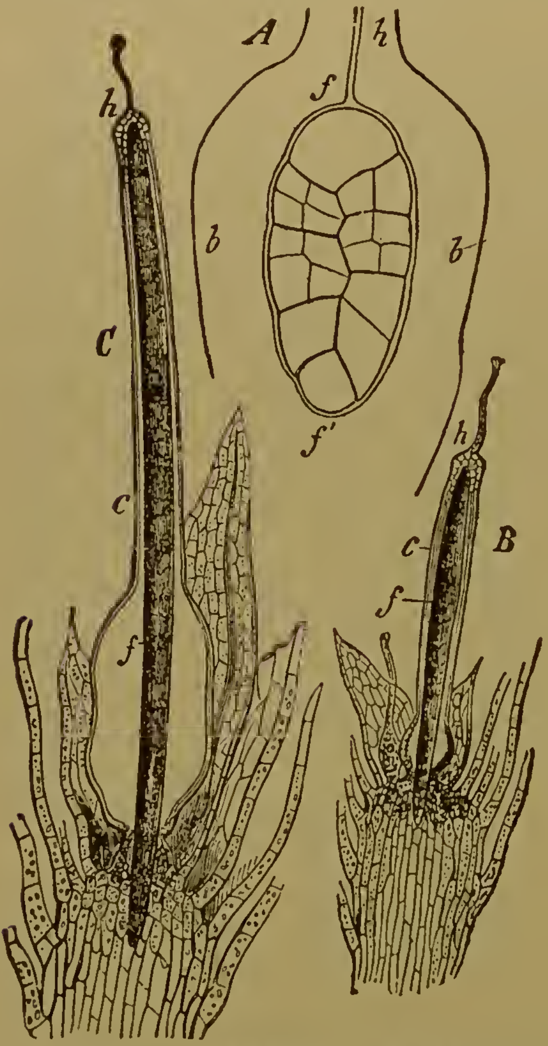

Fig. 125 I. — *Funaria hygrometrica.*
Three stages of the developing sporogonium (*ff′*); *bb*, ventral portion. *h*, neck, of sporogonium. The base (*bb*) forms the calyptra *c* (*C*). (*A* × 500, *B* and *C* × 40.) (After Sachs.)

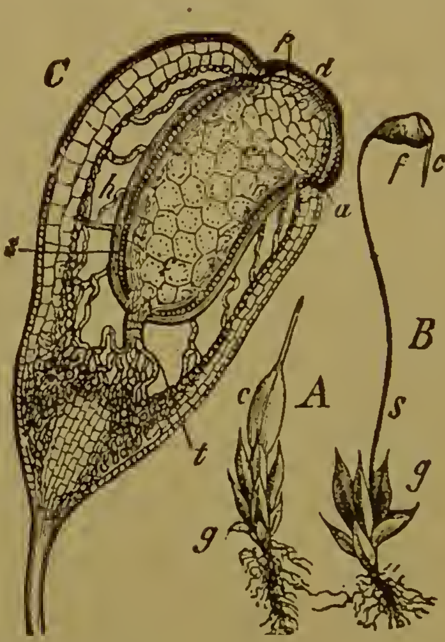

Fig. 125 II. — *Funaria hygrometrica.*
A, Shoot bearing an immature sporogonium, *g*, with calyptra *c*, upon the capsule. *B*. Nearly mature sporogonium; *f*, capsule with calyptra *c*; *s*, seta (stem). *C*, Longitudinal section of sporogonium; *cc′*, columella; *s*, spore-forming layer; *h*, air-cavity; *a*, the ring (annulus) below the lid (operculum); *p*, "peristome." (After Sachs.)

well as those already referred to, will assist in further elucidating these relations.

A fern-prothallium with a young sporophytic fern-plant is shown in Fig. 126. This young plant is the result of the fertilization of the archegonium. The root is seen at *w*, the first leaf at *b*.

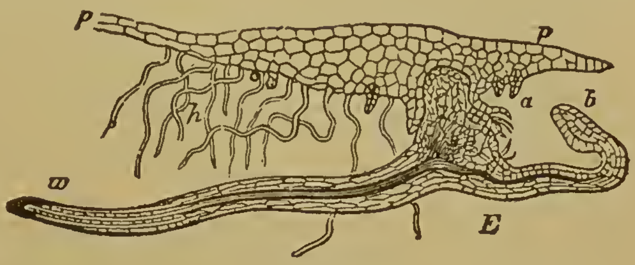

FIG. 126.
Adiantum capillus-veneris. (After Sachs.)

We will now compare vascular cryptogams and phanerogams (Fig. 127, 1 and 2). The ruled rectangle represents the period of separation from the mother-plant and winter-rest; *S* represents the asexually produced macrospore and the embryo-sac; *E* is the egg-cell. ♂ Represents the microspore in 1 and the pollen-grain in 2.

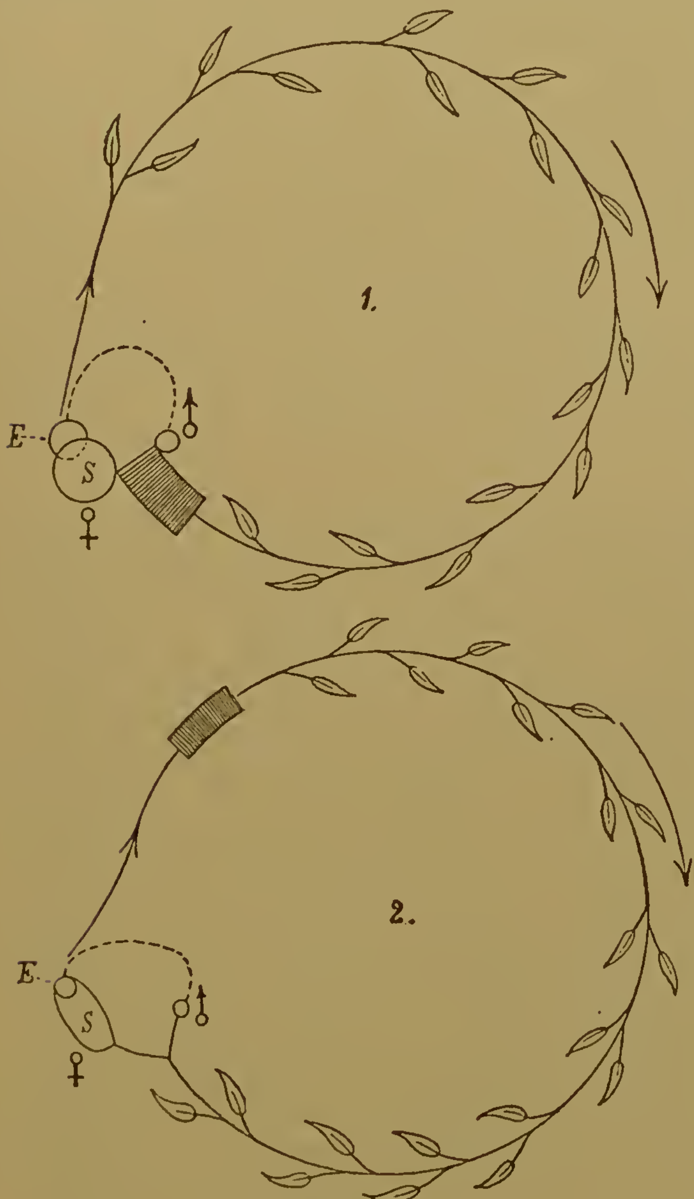

FIG. 127.

The beginner will be surprised to learn that the entire phanerogamic plant with its flowers represents the asexual generation. If this be so, where is the sexual generation? Its existence is limited to a minimum of space and time. In its behavior it is markedly different from the corresponding generation in the vascular cryptogams. Let us consider that which is analogous and that which is not analogous. The embryo-sac and the pollen-grain are indeed represented by analogous structures in the vascular cryptogams; such analogies are the most marked in the "heterosporous" cryptogams, whose sexually different spores have different prothallia. The larger spores, *macrospores*, produce the archegonia, corresponding to the embryo-sac and egg-cell. The smaller spores, *microspores*, produce the fertilizing element, similar to the pollen-tube of pollen. Let us now consider the differences. The macrospore becomes separated from the mother-plant and for a time leads an independent existence during which it germinates and produces archegonia. The *embryo-sac* of gymnosperms, of the phanerogams in particular, remains in union with the mother-plant. It is enclosed by the coverings of the ovule, which usually appear as the parts of a peculiarly modified leaf. The entire ovule as well as the perfected pollen-grain are structurally arranged so that the egg-cell in the embryo-sac may be formed and fertilized while still in union with the mother-plant. After fertilization the egg-cell undergoes division and develops into the embryo of the future plant. Both the embryo-sac and macrospore possess sufficient reserve food-material to make the formation of the embryo possible. When the embryo is fully formed, it becomes separated from the mother-plant and after a period of rest germinates and develops into a new plant. It is possible to distinguish a neck and a basal portion of the so-called "archegonium" of gymnosperms, as in the archegonium of ferns.

The *microspore* is separated from the mother-plant, likewise its equivalent, the pollen-grain. However, the "germinating" microspore of *Selaginella*, a vascular cryptogam, produces an entirely different structure from that produced by the germinating pollen-grain, although there is a marked external similarity. In vascular cryptogams fertilization takes place in water; motile spermatozoids with spirally wound plasmic cilia are formed. The pollen-tube, a single non-septate slender filament, is formed from the pollen-grain. Air-currents, insects, etc., carry the pollen-grain to the moist stigma of the pistil, where it germinates, sending out the above-mentioned pollen-tube, which penetrates the soft tissues of the stigma and style, finally reaching the cavity of the ovary, where it enters through the openings in the seed-coats (mĭcropylar opening); here it comes in contact with the apex of the body of the ovule and embryo-sac, and finally the egg-cell. The morphological appearance of the developing pollen-tube is wholly different from the development of the microspore. Their internal structure, which is also wholly different, we will not discuss. Neither a supporter of the theory of descent nor any physiologist can at the present time hope to solve the question—What changes are necessary in the idioplasmatic structure in order that a microspore which regularly forms motile fertilizing elements may develop a fertilizing tube like that of the pollen-grain?

The so-called "vegetative" cells which regularly appear in the pollen-grains of conifers are looked upon as evidence in favor of the theory of descent. These pollen-grains are several-celled, but only one cell develops into the pollen-tube. The remaining cells are supposed to be a "rudimentary male prothallium." The microspore of *Selaginella* is also several-celled, and has a vegetative cell. Anxious searchers for phylogenetic characters will naturally allow themselves to become blinded by factors apparently in their favor. Even in the present state of our knowledge on the subject I will venture the statement that the contents of the vegetative cells in the pollen-grains of conifers, etc., serve to nourish the cell which develops into the pollen-tube. According to JURANYI, one of the vegetative cells contains starch.[1] ELFVING[2] states that the vegetative cell of *Leucoium æstivum* is reabsorbed, while its nucleus as well as the nucleus of the reproductive cell is later found in the pollen-tube. Other observations teach that very long cells, such as the laticiferous tubes and the bast-cells, are frequently multinuclear. It must also be remembered that the pollen-grain of conifers requires a long time to reach its destination, hence must have some food-supply.

In *Selaginella*, which contains two kinds of spores, the macrospore separates from the mother-plant *before* the formation of the archegonia. The germinating macrospore which develops sterile archegonia is not equivalent to the germinating seeds of phanerogams, but rather to the embryo-sac, which is not adapted to become separated from the mother-plant, hence does not separate, and forms its egg-cell apparatus near the apex, in the most suitable location for fertilization. From the above considerations of reproduction we see that that which is *physiologically equivalent* may differ very widely *morphologically*. The ripe seed of phanerogams will at once develop into a leafy plant while the mature macrospore must be fertilized before it can develop into a new plant; from this it is clear that structures which resemble each other *morphologically*[1] may be totally different *physiologically*. The names macrospore and microspore, embryo-sac and pollen-grain, should therefore be retained as parallel terms. If one purposely ignores what has just been stated, especially that among vascular cryptogams the sequence is separation from the mother-plant and subsequent fertilization, while the reverse is true of gymnosperms, it can be seen how the advocates of the theory of natural descent can assert that the gymnosperms may be classed with the vascular cryptogams as well as with the phanerogams,[2] that is, that they are midway between the two great divisions.

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[1] Pringsheim's Jahrbücher, VIII, 1872.

[2] Studien über die Pollenkörner, etc., Jen. Zeitschrift f. Naturwissenschaft, XIII (new series).

Because of the importance of this subject we will add the following statements.

From what has been said it would be wrong to conclude that a slight change in the behavior of the macrospore would suffice to prove the phylogenetic derivation of gymnosperms from the vascular cryptogams. Let us consider briefly what these changes would be and what changes should not take place. In order that *Selaginella* may arrive at the cycad-stage the macrospore must not adapt itself to become separated from the mother-plant nor undergo a period of rest until it has been fertilized by the suitably organized microspore. After this change had been brought about separation from the mother-plant could follow, and the disposition to undergo a period of rest should now become manifest. In order that the macrospore might remain in union with the mother-plant it must undergo an *entirely different* mode of development. What slight similarity exists between the *Cycas*-ovule and the sporangium of *Selaginella* is evident from GÖBEL's statement that the *integument* of the *Cycas*-embryo has no analogue among vascular cryptogams, and therefore he calls it a "neo-formation." This investigator is certainly authority on subjects pertaining to comparative morphology. The macrospores of the *Cycas*-sporangium are not formed by the mother-cell dividing into four, as in the *Selaginella*. In regard to the cuticularization of the outermost layer of the wall of the embryo-sac, it may be said that it is of importance in the processes of nutrition, as is evident from my investigations in regard to the "antipodal" cells. It aids in conducting food-materials along definite paths. It has not been demonstrated that such cuticularization owes its origin to "phylogeny."

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[1] It should be remembered that such morphological similarity or dissimilarity of organs which seem dissimilar or similar physiologically is often only apparent, and not *real*.—TRANS.

[2] SACHS, Vorlesungen, p. 913; GÖBEL, Grundzüge der Systematik, p. 1.

I will close this discussion with the following statement: If the great gulf between vascular cryptogams and gymnosperms did not exist, it would not have been necessary for the genius of HOFMEISTER (in 1851) to introduce a *tertium comparationis* in the great plant-groups, the vascular cryptogams and gymnosperms.

It is now necessary to explain some of the special adaptations for reproduction and development among the vascular cryptogams.

The *sporangia* of vascular cryptogams usually occur in small groups (*sori*) upon the lower surface of the leaf, or as shield-like organs on supports, as in *Equisetinæ*. Up to the time of maturity these sporangia are usually covered by a protective organ, the *indusium*, or more rarely by the curled margin of the leaf. The sporangia contain the spores. In the mature sporangia of many ferns (Fig. 128) there is noticeable an incomplete median ring of thickened cells. By a sudden mechanical movement (hygroscopic movement) this ring aids in ejecting the spores.

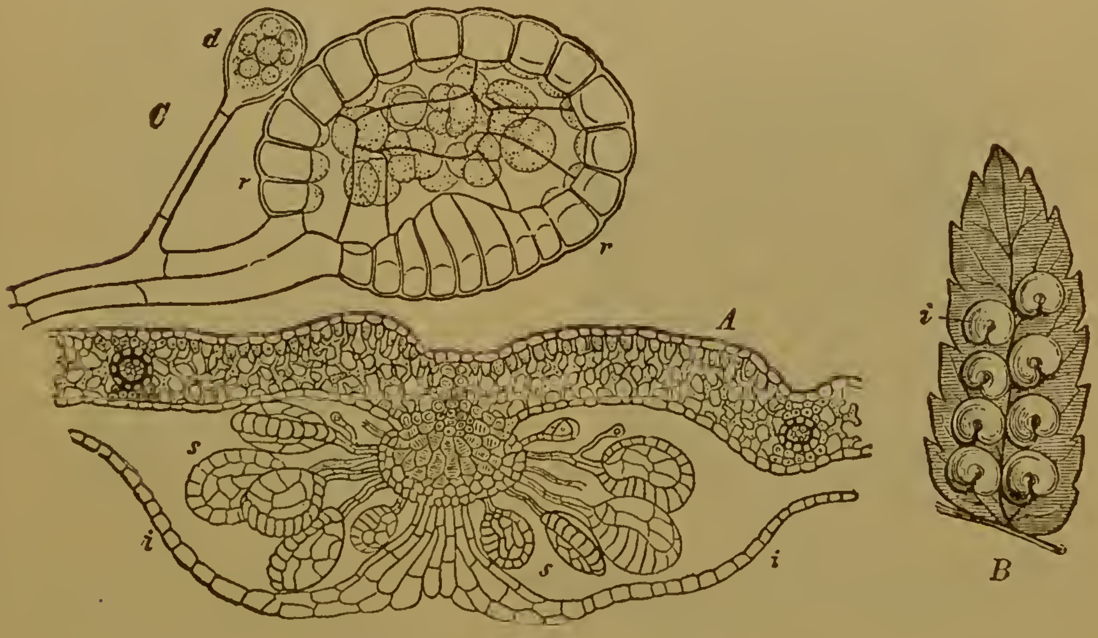

FIG. 128.—*Aspidium Filix mas.*

A, Vertical section of a sorus *ss* with indusium *i*; *B*, pinnule with sori; *C*, single immature sporangium; *d*, glandular hair. (After Sachs.)

In Fig. 128, *C*, it is noticeable that the ring extends from *r* at the left of the base of sporangium to *r* at the right. The cells of this ring, when mature, are considerably thickened along the inner side, as well as in the radial direction (vertical to the surface of the figure).

Fig. 129 shows the product of the fertilized archegonium. The egg-cell has developed into a young plant with leaf, stem, and root (*b*, *s*, *w*). The foot (*f*) of the embryo absorbs the food-material (starch) of the spore at *c*; *i* is the inner, *ex* the outer, spore-membrane (exospore). The prothallium *pt* shows the root-hairs

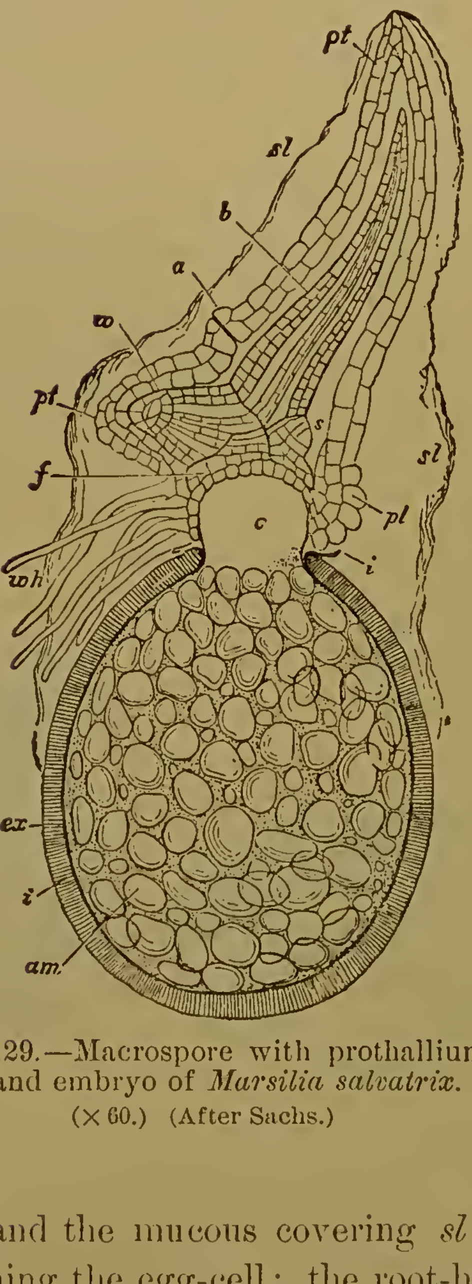

FIG. 129.—Macrospore with prothallium and embryo of *Marsilia salvatrix*. (× 60.) (After Sachs.)

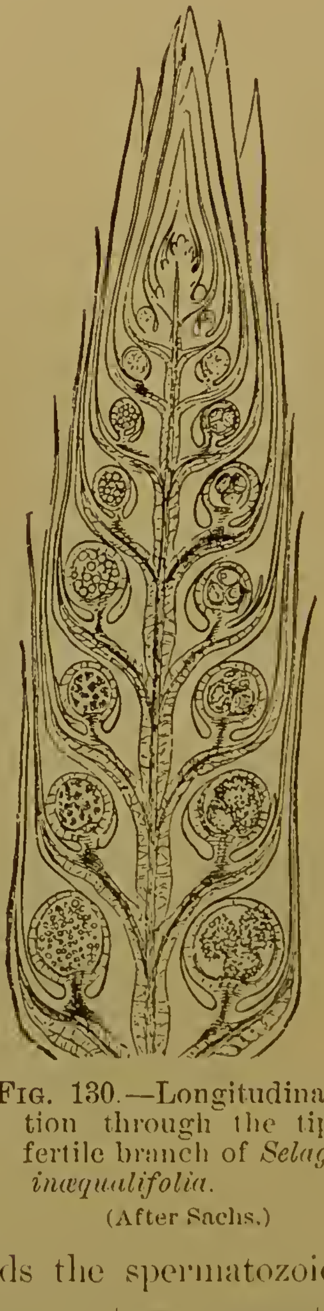

FIG. 130.—Longitudinal section through the tip of a fertile branch of *Selaginella inæqualifolia*. (After Sachs.)

wh, and the mucous covering *sl* which aids the spermatozoids in reaching the egg-cell; the root-hairs serve as a temporary attachment to the soil at the bottom of the water. Fig. 130 shows a fertile branch of *Selaginella inæqualifolia*, with macrosporangia and microsporangia.

Finally, in reference to what has been stated and what remains to be considered, we will add the following in explanation of the diagramatic figures (131 and 132). Both refer to the phanerogams. In the figure (129) of *Marsilia* and that of gymnosperms (131) we at once notice the provision made for the nourishment of the embryo. The embryo is entirely surrounded and connected with the nutritive tissue, the *endosperm*. Fig. 132 represents the process of fertilization among angiosperms. In *Marsilia* and the gymnosperms the endosperm exists before fertilization, while in the angiosperms it is formed after fertilization. Recent investigations by the author[1] resulted in the probable conclusion that the "antipodal apparatus" which exists before fertilization is not a "rudimentary" organ, but a peculiar structural arrangement to serve in nourishing the developing embryo. Until recently the antipodal cells were considered as being without any physiological function, but of sufficient value to indicate a "phylogenetic rudiment." As indicated, the subject is perhaps capable of an entirely different interpretation. There are cases (*Salvia pratensis*, *Zea Mays*) in which the so-called antipodes prove to be

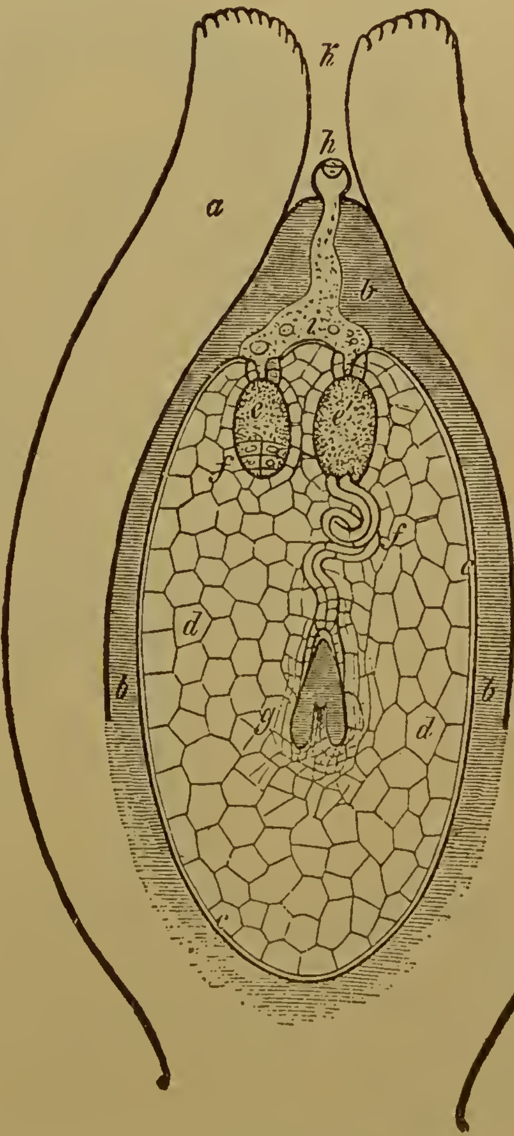

FIG. 131.—Diagramatic longitudinal section through the ovule of a gymnosperm.
(After Sachs.)

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[1] Zur Embryologie der Phanerogamen, insbesondere über die sogenannten "Antipoden." Nova Acta d. Ksrl Leop. Car. D. Ac. d. Naturf. 1890 (The Embryology of Phanerogams, with special reference to the so called "Antipodes").

the primordial endosperm-cells, since they unite with the remaining endosperm immediately *after* fertilization. (For further particulars refer to the work cited below.) In conclusion I will add that the antipodes also indicate a nutritive function by their position and arrangement.

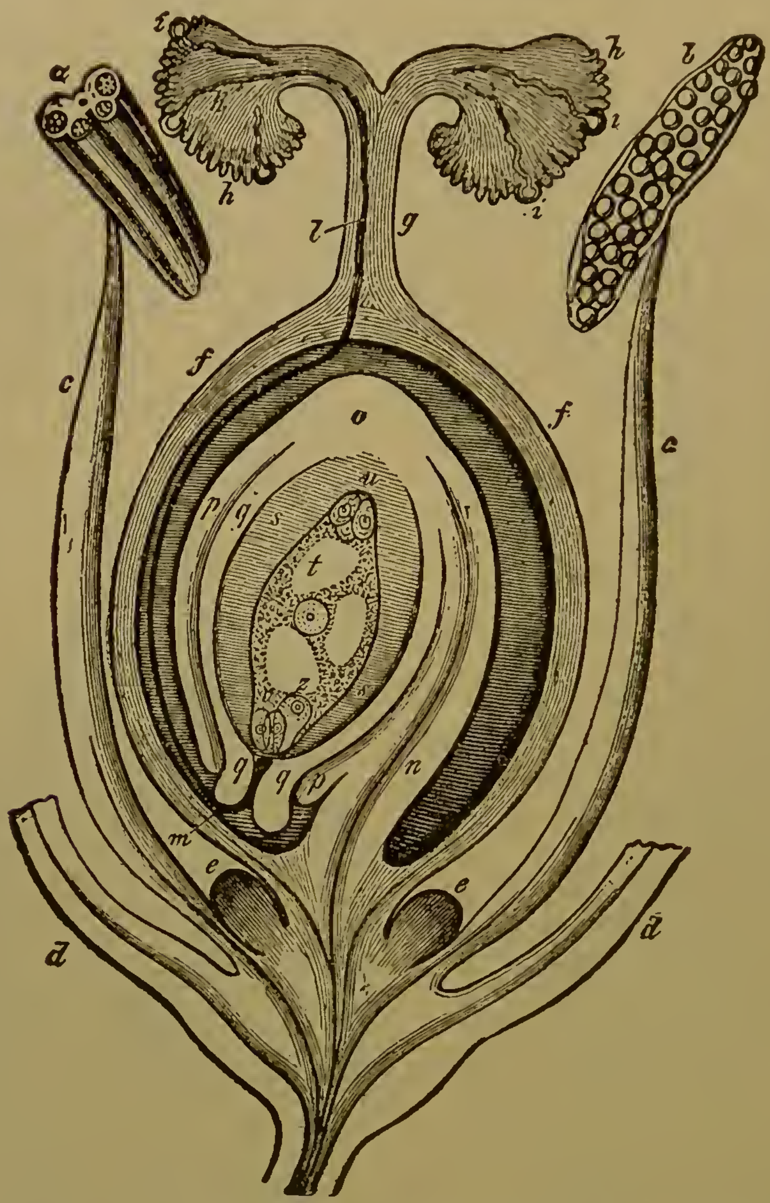

FIG. 132.—Diagramatic longitudinal section through the flower of an angiosperm. (After Sachs.)

GYMNOSPERMS AND ANGIOSPERMS.

As is well known, the phanerogams are divided into the great groups *gymnosperms* and *angiosperms*.

What has already been said, especially in reference to the above diagramatic figure (131), will aid in understanding the following particulars in regard to the process of fertilization among gymnosperms. A pollen-grain (*h*) is carried by the wind to the opening left in the integument of the embryo, namely, the micropylar opening (*k*). This is made possible by the position of the ovules at the inner side of the base of the seminiferous scale, as shown in Fig. 133. The scales mutually cover and protect each other, yet the pollen-grains may get between them at certain times. At first the pollen-grain is found near the upper part of the seminiferous scale adhering to a sticky fluid which is secreted at this time. This fluid is carried downward, and with it the pollen-grain. Soon the pollen-tube begins to form and passes through the nucellus (*b b*), finally reaching the archegonia. (The time intervening between pollination and fertilization is an entire year for many gymnosperms.) *e* and *e′* (Fig. 131) show the immediate results of fertilization. In *e′* the egg-cell of the archegonium has developed into a filamentous structure (*f*), the "suspensor," on the end of which the embryo is formed. The suspensor serves to push the embryo into the endosperm. The structure of the archegonia, as well as the fact that the embryo-sac is filled with endosperm *before* fertilization, places the gymnosperms nearer to the vascular cryptogams than to the angiosperms. Such a relative position cannot be denied, but the recognition of such a relation is simply a *process of thought* which the comparative study of the plant-series creates in our minds; that such a series is *genetic* is an unverified postulate of the dogmatic teaching of descent which allows fantasy to supplant that which empirical investigations leave unanswered.

As has already been observed, the embryo of gymnosperms is not unprotected, as the name would indicate. Among pines and firs, for example, the leaf-organs which bear the ovules, hence the "carpides" or "carpels," are enabled by their position and arrangement to cover each other. The morphological significance of the cone-scales was formerly the cause of considerable scientific controversy. A small leaf-scale (keel) supports the much larger seminiferous scale as a ventral excrescence. In Fig. 133, *A*, *d* represents the leaf-scale; the large seminiferous scale in *B* bears the ovules *b b*, which later form

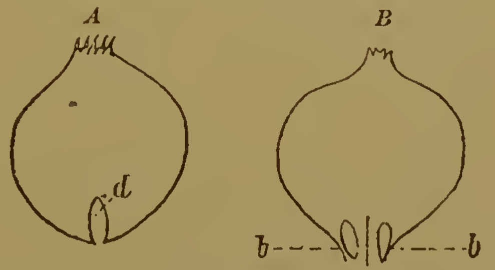

Fig. 133.

A, Scale of conifer seen from without; *B*, scale of conifer seen from within.

the ripe seeds variously equipped with winged appendages for the purpose of facilitating their distribution by air-currents. Eichler for a long time considered the seminiferous scale as a "metamorphosed shoot." The entire cone would therefore be the *inflorescence.* Now the entire structure is considered to be a single female flower, which bears numerous peculiarly modified seed-leaves on one axis. Strasburger made a special study of conifers.

We will here note that the stem-structure and the mode of axillary branching represent further differences between conifers and angiosperms. Concerning the differences between the male flowers of gymnosperms and angiosperms we will give further particulars in the discussion of *stamens.*

In distinction to gymnosperms the ovule of angiosperms is usually situated *at the margin* of the carpel; the latter organ is not flat, but typically arched, forming a hollow structure (the ovary). This organ may be formed from a single carpel or by the adhesion (growing together) of several carpels. These several carpels are so united that the ovules inserted in the margins come to lie in the interior of the cavity so formed. The united margins on which the ovules are inserted are known as *placentæ.* This adhesion of parts, which does not exist in gymnosperms, because it is not required, necessitates still other structural adaptations for the purposes of pollination and fertilization. Since the ovary is closed, the pollen cannot be brought to the micropyle by the wind or insects. There is a special organ, the stigma (Fig. 132, *h*), which receives the pollen-grain; also a second organ, the style (*g*), which forms the path for the growing pollen-tube (*k l m*). The seed-leaves (carpels) by their union form a longer or shorter canal at the upper part known as the stylar duct (Griffelkanal). This channel, which is either hollow or composed of soft tissue, is bounded above by the papillose terminations of the carpellary leaves, which constitute the *stigma.* These terminations may differ greatly morphologically; they may appear as fine rays, papillæ, etc. The stigma secretes a moist sticky substance to which the pollen-grains adhere and in which they begin to germinate. The pollen-tube extends down the stylar duct into the cavity of the ovary; special structural adaptations may also exist for conducting the growing pollen-tube to the micropylar opening. In reference to the explanation of Fig. 132 the following is added: *a*, transverse section of anther; *b*, longitudinal section; *c*, filament; *f*, wall of ovary; *n*, the funiculus; *o*, base of the embryo; *p* and *q*, outer and inner integument; *s*, nucellus; *t*, embryo-sac; *v*, and *z*, egg-cell apparatus (synergidæ); *u*, antipodes; *e*, nectaries; *d*, basal portion of the floral envelopes.

For the time being we will discontinue the discussion of the further processes and products of fertilization; they will be referred to at the close of III and in chapter IV of this section. We shall now take up the consideration of the general morphology and physiology of the phanerogamic flower.

III. THE PHANEROGAMIC FLOWER.

Although the "moss-flower" has both sexual organs upon the same axis, it is not analogous to the hermaphroditic flower of phanerogams, which also bears carpels and stamens on one axis. We know from what has already been stated that the *spores* of the moss-sporangium have an origin analogous to that of the *embryo-sac* and the pollen-grains. The formation of the germinal vesicle in the embryo-sac, and the divisions and other processes which prepare the pollen-grain for germination, correspond to the sexual generation represented by the development of the leafy moss-plant.

We will now make a comparative study of the following phanerogamic flowers: (1) the female flower of a pine, *Picea excelsa;* (2) the flower of rye, *Secale cereale;* (3) the hyacinth, *Hyacinthus orientalis;* (4) the cherry-flower, *Prunus Cerasus.*

Number 1 represents the gymnospermous flowers; 2 represents not only the *gramineous* flower, but all monocotyledonous flowers with colorless corollas; *Hyacinthus* is an example illustrating the apetalous monocotyledonous and dicotyledonous flower. Finally, *Prunus Cerasus* represents the type of the apparently "most perfect" flower, equipped with calyx, corolla, stamens, and carpels (pistils).

In the discussion of leaf-organs (Part III, B, 2) the floral leaves were very briefly touched upon. We shall now enter into a more thorough discussion. By introducing physiological factors we will be able to overcome the disagreeableness of mere dry description.

A. Calyx, Corolla, Nectaries. The Flower as a Whole.

In *Picea excelsa* the ovules are protected by the overlapping of the cone-scales. We have learned that the torus with the style and stigma is not necessary in this case. Because of the firmness and arrangement of these scales no *calyx* is necessary (among ♂ flowers bud-scales protect the stamens). Since fertilization is brought about by the wind, a colored corolla is also unnecessary—the color serves to attract insects; the nectaries are likewise absent, their function being to attract insects. Petals are also absent from number 2. In numbers 3 and 4 they are present, because hyacinths and cherry-flowers, as well as thousands of other colored flowers, are dependent upon insects for pollination. The conditions of reproduction in spite of hermaphroditism (in 2, 3, and 4) are so regulated that the great majority of hermaphroditic or bisexual flowers are dependent upon cross-fertilization. In only a very small number of cases has it been found that self-fertilization is more beneficial.

The pine (1) is diœcious. Since the wind is the means by which pollination is brought about (anemophilous), it is evident that pollen must be very plentiful to insure fertilization; this we find to be the case. Sometimes pollen-grains possess vesicular enlargements of the exine which facilitate their distribution by the wind (Fig. 134, *bl*).

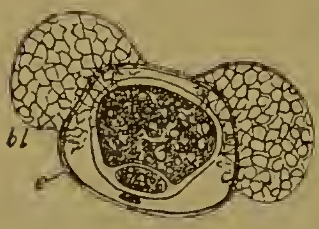

Fig. 134.—Pollen-grain of *Pinus Pinaster*. (After Sachs.)

In the anemophilous *Gramineæ* (2) the pollen-grains are caught and retained by the delicate bristles of the stigma (see Fig. 135). The small scales at the base of the stamens, the so-called "lodiculæ," have a mechanical function; by *swelling* they assist in opening the flower. At least they need not be considered as forming a "rudimentary" perianth or calyx, since the bracts or glumes take the place of the calyx. As a rule, each individual flower has two secondary bracts (*paleæ*) and each spikelet has two primary bracts (glumes). It would be wholly wrong to suppose that the flower of the conifers or grasses is rudimentary or imperfect as compared with the flower of the cherry-tree.

Numbers 3 and 4 represent types of flowers whose pollen is carried to the stigmas of other plants of the same species, and they in return receive pollen from other plants. The transfer is made by insects, and such flowers are said to be *entomophilous*. The petals of the corolla are either united or free in the different groups of angiosperms. They often have peculiar adaptations of form to facilitate the fertilization by insects. Different odors, sometimes pleasant and sometimes very disagreeable, as well as various glandular secretions (nectaries) serve a to attract insects.

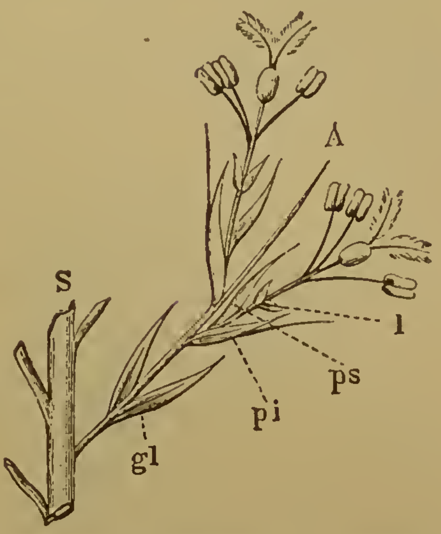

FIG. 135.—Spikelet of rye with two flowers.

S, Spike; *A*, spikelet; *gl*, glumes of spikelet; *pi* and *ps*, lower and upper glumes of the flower; *l*, lodiculæ (swelling organs). Terminating in three stamens and the pistil.

Why the organ known as *calyx*, which may consist of either separate or united *sepals*, is absent in number 2 has already been explained. In *Hyacinthus* there is no differentiation into calyx and corolla, while both are present in *Prunus* (4. See Fig. 138). The calyx by its position and greater firmness protects the younger and more delicate parts of the flower. It would, of course, be functionless if other organs were adapted to perform this protective function. There is besides *Hyacinthus* a large series of monocotyledonous flowers in which the calyx is normally absent. Floral coverings which consist of equal or nearly equal leaf-like organs without any distinction as to calyx and corolla are known as the *perianth*. In its appearance it may resemble either the calyx or corolla. It is remarkable that these "apetalous" monocotyledons (orchids, aroids, onions) are equipped with larger or smaller hypsophyllary leaves in the axils of which the young individual flower (orchids) or the young inflorescence (aroids, onions) finds a suitable protection. Further, it is noticeable that among many of the apetalous flowers the rather firm perianth-leaves are green at first and enclose the flower-bud; later they unfold and take on bright colors. In the first stage they resemble the calyx in appearance and function; in the second stage they resemble more nearly the corolla. In *Fritillaria imperialis*, a plant belonging to the same group as 3, special organs occur at the base of the perianth-leaves which secrete a saccharine liquid; they are known as *nectaries* and are found in various flowers. Their function has already been mentioned, but will again be referred to in the discussion of cross-fertilization.

From the foregoing we may conclude that there are parts of the flower which serve the function of reproduction directly, and parts which aid indirectly. To the first belong the *gynæcium* and the *andrœcium*, that is, the *male* and *female* sexual organs of the flower. The calyx, the corolla, the perianth, the nectaries, and the hypsophyllary leaves aid reproduction indirectly, since these organs may be substituted for one or the other of the inessential organs. The flowers of the pine require no calyx, no corolla, no nectaries, or torus. All such structures would be without a purpose. The flowers of grasses require no calyx, corolla, or nectaries, as their absence indicates. A monocotyledonous flower with a perianth, as the hyacinth, may also be without calyx. Flowers of *Prunus* as well as those of many other phanerogamic plants require calyx, corolla, and nectaries for the purposes of reproduction, as is indicated by their presence. Nature does not produce any useless structures.

Number, form, and arrangement of floral organs and their parts play a very important rôle in the morphology of flowers and in the classification of plants. What LINNÉ so fortunately considered to be of importance in establishing his system of phanerogams is embodied in its essentials in our present system of classification; that is, the recognition of *constant* floral characteristics, such as number, cohesion of parts, size, symmetry, etc. The following is a brief summary of such characteristics.

If the calyx, corolla, stamens, and pistils succeed each other vertically on one axis (*receptacle* or *torus*), we have what is known as a *hypogynous* flower. The *ovary* is said to be *superior* (Fig. 136).

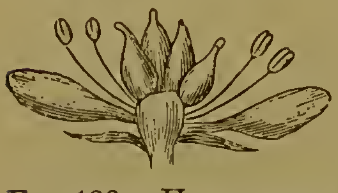

FIG. 136.—Hypogynous flower (*Ranunculaceæ*). (After Berthold and Landois.)

In the second case (Fig. 137) the development of the floral axis is such that the apex appears depressed, that is, a peripheral wall rises above the apex, so that in the mature structure the ovary with its ovules lies below the base of the insertion of the stamens and petals. Such a flower is said to be *epigynous; ovary inferior.*

Finally, in the third case (Fig. (138) the stamens and petals surround the ovary. Such a flower is said to be *perigynous.* The floral axis is also depressed, but the ovary differs from case 2 in that it is "free." In the case of epigyny, according to GÖBEL's investigations, the cup-shaped floral axis is lined on its inner surface by the basal parts of the floral envelopes. These floral envelopes have a strong intercalary growth, soon enveloping the ovary, with the exception of the terminal portions of the styles and stigma. In the perigynous flower the intercalary growth of the cup-shaped axis is perhaps a little below the insertions of the floral coverings, that is, the floral insertions are so near the apex of the torus that they are not affected by the intercalary growth; hence the torus is not enclosed by the floral coverings. Forms intermediate between epigyny and perigyny are not wanting.

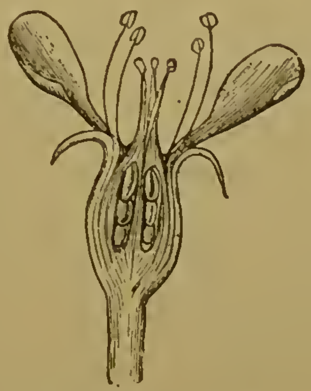

FIG. 137.—Epigynous flower (apple).
(After Berthold and Landois.)

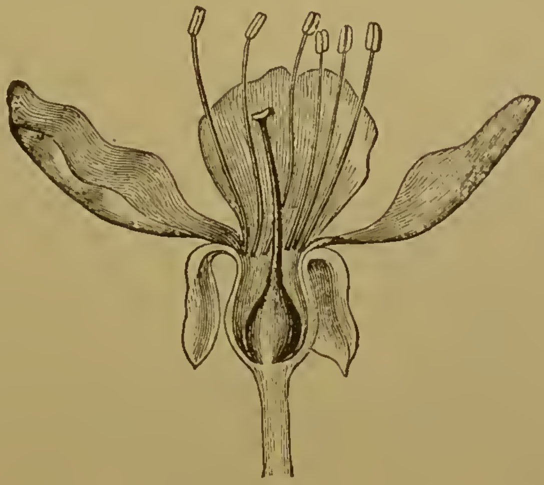

FIG. 138.—Perigynous flower (cherry).
(After Berthold and Landois.)

The individual parts of the flower may be *free* or *united;* sometimes the organs are free below and united (by growth) above, as, for example, the stamens of the *Compositæ.* The number of floral parts differs greatly in different flowers. For example, the stameniferous flower of *Euphorbia* has but one stamen, while the flowers of the *Nymphaceæ* may have more than one hundred.

The number three prevails in the floral elements of monocotyledons. The numbers vary among dicotyledons, though *fives* are very common.

According to the *arrangement* of floral leaves we may recognize the following forms of flowers.

1. *Cyclic* flowers: the elements of one kind of floral leaves

are in the same horizontal plane, "verticillate." Example: the *Liliifloræ*.

2. *Acyclic* flowers: spiral arrangement of the floral leaves. Example: *Magnolia*.

3. *Hemicyclic* flowers: the floral organs may in part be spirally arranged (especially the calyx) and in part verticillate. Example: *Ranunculaceæ*.

The calyx usually forms *one* circle of floral leaves; the corolla also one; the andrœcium one or two; the gynœcium usually one. For causes more or less associated with the mechanical theory of phyllotaxy there is often noticeable an *alternate* arrangement of members of the various verticillæ, provided they occur in equal numbers (see Fig. 139). The whorls or verticillæ may also be *opposite*, as shown in Fig. 140.

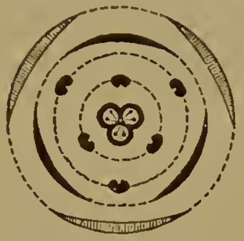
FIG. 139.—Diagram of the flower of *Lilium*. (After Krass and Landois.)

A further discussion of these relations would soon lead us to that stage of investigation in which the comparative morphology of flowers seems to give evidence of the transmutation of one genus into another. We will cite an example. Normally the *Scrofulariaceæ* have five stamens; *Veronica* has two; *Gratiola* has two normal stamens and two sterile structures, the so-called "staminodia." *Digitalis* and *Scrofularia* have four stamens and one staminodium. It is evident that the abortion or the suppression of stamens plays an important part in the cases mentioned. By this "suppression" is meant the non-appearance of an organ which one would expect to appear according to reasons deduced from comparative morphology. In some cases an entire whorl may be suppressed or fail to appear. In other cases there is not a suppression of members, but an increase in the normal number of parts ("*dédoublement*").

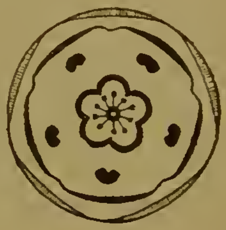
FIG. 140.—Diagram of the flower of *Primula*. (After Krass and Landois.)

Since SCHUMANN[1] has applied SCHWENDENER'S contact theory to the processes of growth and development in the floral region of the plant the investigations in regard to this subject have been placed upon a firmer foundation, while the play of fancy is to a certain extent checked. The exact history of development, the study of which is in every case a difficult and tedious work, teaches that, for example, the first primordia (protuberances) are acted upon by various mechanical influences which give rise to superposed whorls. I have no cause to enter into a discussion of the conditions met with in the flowers of *Scrofularia*, because I do not know any more about the origin of this genus than any one else does.

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[1] Neue Untersuchungen über den Blütenanschluss, Leipzig, Engelmann, 1890.

Before entering into the discussion of the important relations of the floral structure it is important to remember that the great variety represented in the structure of flowers and fruits can no longer be relegated to mere description, but must be considered according to physiological adaptations. Although this change in our science is comparatively recent, we are already enabled to give physiological interpretations to many of the structural modifications; always from a teleological standpoint. The purpose of *many* of these modifications is to insure the most suitable pollination and fertilization. Under this category belong the following structural modifications.

A flower is said to be *polysymmetrical* or *actinomorphic* when it may be symmetrically divided in at least two planes. (Slight differences are not considered.) Illustration: the diagram (Fig. 139) of *Lilium*. A flower is *zygomorphic* or *symmetrical* when it can be divided symmetrically in only one plane. Sometimes there is no plane of symmetry, when the flower is said to be *azygomorphic*. The diagram of the labiate flower is an excellent example of a zygomorphic flower (Fig. 142). The zygomorphic flowers are nearly always lateral. If a plant with zygomorphic flowers should have a *terminal* flower, it is actinomorphic. (*Linaria vulgaris* frequently shows this phenomenon. Such terminal flowers are said to be *peloric*.[1])

The plane of symmetry of zygomorphic flowers usually, but not always (*Solanum*, *Æsculus*), coincides with the *median plane*. The majority of flowers are therefore *median-zygomorphic*. The median plane is that plane which bisects the axis of growth of a lateral member as well as the axial member. Only a few flowers are transversely zygomorphic; that is, the plane of symmetry and the median plane form an angle. In many orchid-flowers the ovary or style rotates about its axis 180°, which brings the young zygomorphic flower in a suitable position to be visited by insects. Fig. 141 illustrates the phenomenon of "resupination." The above-mentioned labiates show this zygomorphy in a marked degree in the *two-lipped* calyx and corolla (Figs. 142 and 143). This

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[1] Lateral peloric flowers are also reported. Whether such lateral position is real or only apparent I am unable to state.—TRANS.

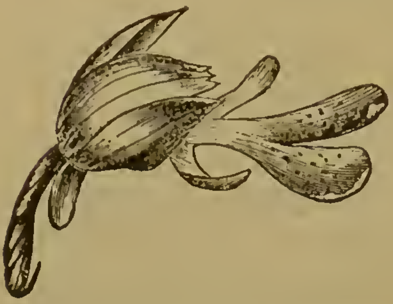

FIG. 141.—*Orchis fusca.*
(After Berthold and Landois.)

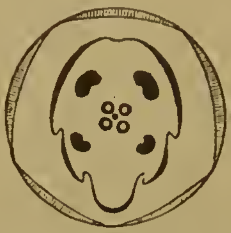

FIG. 142.—Diagram of a labiate flower.
(After Krass and Landois.)

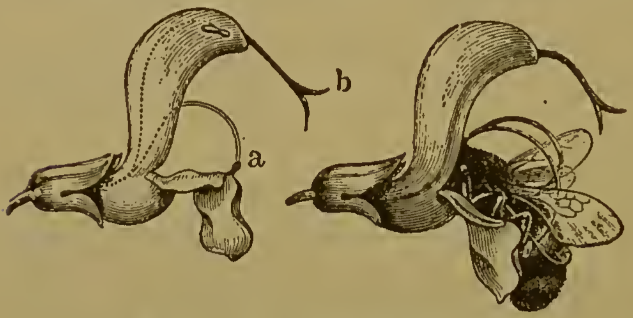

FIG. 143.—*Salvia pratensis.*
a, Anthers; *b*, pistil.

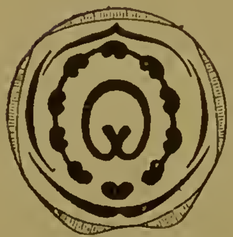

FIG. 144.—Diagram of a papilionaceous flower.
(After Krass and Landois.)

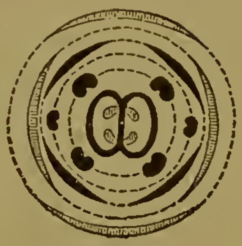

FIG. 145.—Diagram of a cruciferous flower.
(After Krass and Landois.)

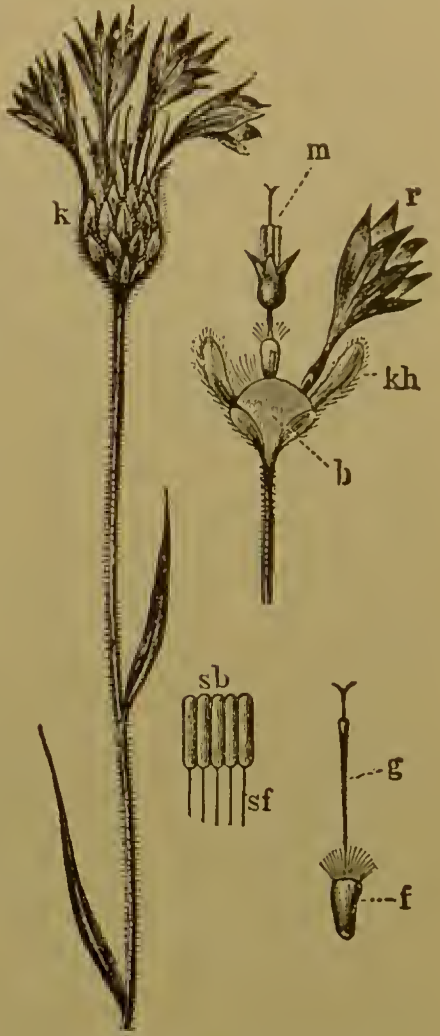

FIG. 146.—*Centaurea cyanus.*
(After Krass and Landois.)

family, which comprises about 2600 species, is widely distributed (EICHLER). The *Papilionaceæ* comprise about 3000 species (Eichler); their floral arrangement is represented diagramatically in Fig. 144.

The *Liliaceæ* represent the actinomorphic type. Of the dicotyledons we shall refer to the *Cruciferæ* (Fig. 145), comprising about 1200 species (Eichler) and distributed throughout the temperate zones.

Among the *Umbelliferæ* as well as the *Compositæ* the flowers of the same inflorescence (*umbel*, head) are often different; the central ones are actinomorphic and the peripheral ones zygomorphic. Among the *Compositæ* there are distinct strap-shaped and tubular flowers, or even two-lipped flowers, in place of the former. Fig. 146, *k*, shows the involucre of hypsophyllary leaves; *m*, a *tubular* bisexual flower; *r*, a sterile *two-lipped marginal* flower; *b*, the receptacle; *kh*, a hypsophyllary leaf; *f*, ovary; *g*, style with stigma; *sf* and *sb*, filaments with united anthers. The *Umbelliferæ* are distributed through the temperate zone and comprise about

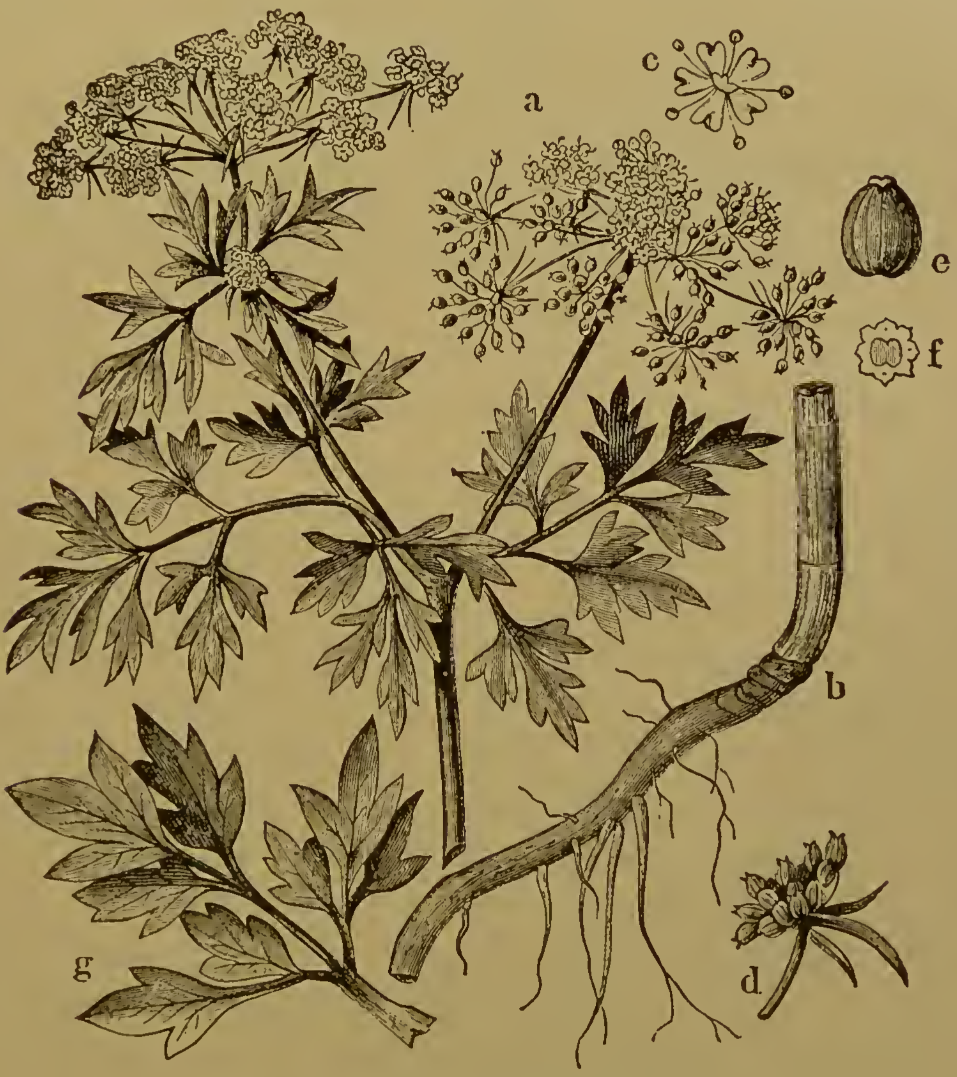

FIG. 147.—*Aethusa cynapium.*

a, Umbel; *c*, flower; *e*, fruit; *f*, cross-section of the fruit; *g*, leaf. (After Krass and Landois.)

1300 species (Eichler). Figs. 147–149 are given to represent the general characteristics of this family.

The dicotyledons are now usually divided into *Choripetalæ* and

Sympetalæ, according to whether the *petals of the corolla* are *free* or *united.* To the former belong the *Cruciferæ*, *Ranunculaceæ*, and *Rosaceæ;* to the latter the *Labiatæ*, *Gentianaceæ*, *Solanaceæ*, *Compositæ*. (See page 61 concerning "sympetalous" flowers.)

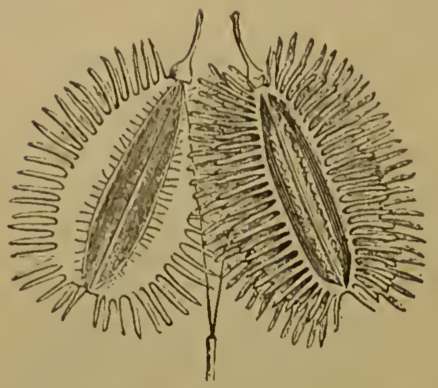

FIG. 148.—Seed of *Daucus Carota* (carrot).
(After Berthold and Landois.)

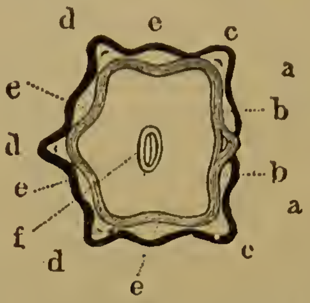

FIG. 149. — *Carum carvi.* Diagramatic cross-section of a part of the seed. *aa*, Contiguous surface, oil-glands near *b* and *e*; *d* and *c*, primary ribs; *e*, secondary ribs with oil-glands.
(After Berthold and Landois.)

We will now consider the structure and function of the *nectaries*, and then pass to the discussion of the *andrœcium* and *gynæcium*.

As already indicated, the *nectaries* serve to secrete a honey-like substance called nectar. This secretion attracts insects, which feed upon it, and by their movements on lighting and attempting to secure the nectar cause the pollen to adhere and alight upon them, to be carried to other plants (of the same species) for the purposes of cross-fertilization. The nectaries are morphologically different in different plants. In *Alchemilla vulgaris* they are located in the calyx, very frequently they are located in the petals, forming the spurs of orchids, *Ranunculaceæ*, etc. In *Caltha palustris* they are located near the base of the ovary; in *Cerastium*, near the base of the filament; among many of the *Liliaceæ* they occur in the septa of the ovaries, and are known as septal glands. Finally, there are nectaries formed by special structural modifications, such as those of *Parnassia palustris* and *Musa paradisiaca.*[1]

Not every insect can secure the nectar of any flower. Certain insects are especially adapted to certain flowers in order to bring about cross-fertilization. The depth of the floral tube and the spur corresponds to the length of the proboscis of the visiting insect. There are also protective arrangements to prevent the visit of *useless* or *harmful* insects. Such are the hair-cells and scaly structures in the corolla, which sometimes makes access to nectaries difficult or impossible (*Labiatæ*, *Asperifoliæ*); also the so-called "masked" corollas, in which the hood of the lower lip is closely appressed to the upper lip (*Linaria*). ANTON V. KERNER, who has made a special study of alpine plant-life, has added to botanical literature two important volumes, entitled "Protective Arrangement of the Pollen against Premature Liberation and Germination," and "The Protection of Flowers against Undesirable Guests." In reference to the latter work (Innsbruck, 1879), I will state that it was above all the author's desire to show clearly the suitable adaptations of the various floral arrangements and to strengthen our teleological conception of nature. We do not see in it any evidence in support of the *theory of selection*, as the author seemed to indicate in the introduction to this work. CH. K. SPRENGEL (1793) made important discoveries in regard to the physiological significance of individual floral parts, especially the corolla and its zygomorphy. He is the discoverer of the law of the absence of self-fertilization. We now know that this "law" is not generally applicable, since there are plants with special adaptations for self-fertilization (see below, cleistogamous flowers).

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[1] Studied more in particular by W. BEHRENS, Flora, 1879. The above statements are based upon the investigations of this author.

B. THE STAMENS AND POLLEN-GRAINS.

The stamens of gymnosperms are in general quite different from those of angiosperms. In the former the part which bears the pollen-sacs is sometimes flat, sometimes peltate or cylindrical; in the angiosperms it is in general filamentous, and is known as the *filament*. Among gymnosperms the number of pollen-sacs is usually much greater and more variable than among angiosperms; two is the usual number in the latter group.

The following discussion of stamens is based upon their appearance among angiosperms. To explain the structure and function of this organ we will give the important characteristics illustrated by a few typical examples.

The elongated portion, *filament*, supports the *anthers* (pollen-sacs). Fig. 150 shows the most frequent form of *dehiscence* or opening of the anther, that is, it splits open in its longitudinal direction; more rarely there are pores formed at the apex, or the apices may open by means of transverse valves. In the *Ericaceæ* we find an interesting arrangement. The anthers open by the formation of pores. The hardened appendages of the anthers assist in the expulsion of the pollen-grains when insects come in contact with them. (See Fig. 152.)

Let us now consider the anther in cross-section—represented considerably magnified in Fig. 153, *A*, *B*. *A* represents the cross-section of an entire anther, in which the valves have separated from the pillar (connective tissue) at *z*. *B* is the very highly magnified portion *β*; *e* is the epidermis and *x* the fibrous mechanical layer. At *y*, *B*, it can be plainly seen that the fibrous layer does not extend quite to the pillar. Anatomically this is the weakest point, and at which separation takes place. The middle portion in *A* in which the vascular bundle lies is called the *connective*, because it serves as a union between the two parts of the anther. Each half may also possess two chambers; the entire anther is therefore either *two-* or *four*-chambered. If one supposes the four chambers to be close together on one side of the connective we have an anther with both longitudinal openings on one side. If the dehiscence is inward (in reference to the flower) the anthers are designated as being *introrse;* if facing outward, they are said to be *extrorse.* A teleological relation which has been studied more in particular by JORDAN[1] is of special importance. The position of the nectaries is dependent upon introrsity and extrorsity,

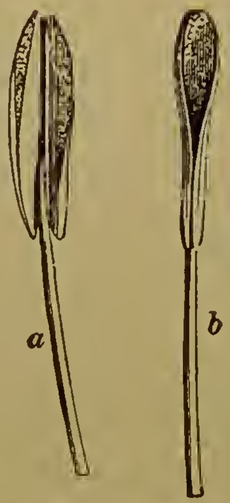

FIG. 150.

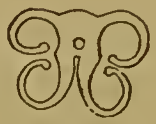
FIG. 151.

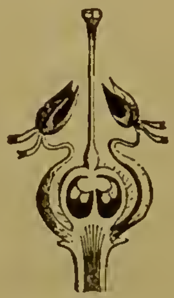
FIG. 152.

FIG. 150.—Anther of white lily.
a and *b*, Modes of dehiscence. (After Berthold and Landois.)

FIG. 151.—Cross-section of an anther (After Berthold and Landois.)

FIG. 152.—Longitudinal section through the pistil and two anthers of *Calluna vulgaris*. (After Berthold and Landois.)

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[1] Die Stellung der Honigbehälter etc. Dissertation. Halle, 1886.

and other relations of the anthers. It need, of course, not be stated that insects perform the act of pollination of plants unconsciously. The place where they are engaged in securing honey is also the appropriate place to come in contact with pollen. The following is from Jordan's communication.

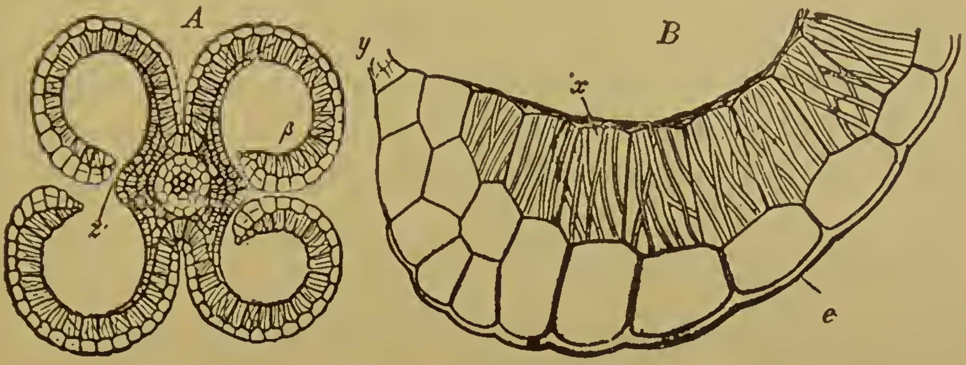

FIG. 153.—Cross-sections of an anther. (After Sachs.)

1. Anthers *introrse.* Nectaries *intrastaminal*, that is, between the andrœcium and the gynœcium; as in *Dianthus Carthusianorum*, *Lychnis dioica*, *Nymphæa alba*, *Comarum palustra*, *Allium Schœnoprasum*, etc.

2. Anthers *extrorse.* Nectaries *extrastaminal*, that is, between the andrœcium and the corolla or between corolla and calyx; as in *Ranunculus acer*, *Tilia grandifolia*, *Parnassia palustris*, etc.

Most interesting are those cases in which the anthers appear to be unsuitably related to the nectaries as, for example, in *Convolvulus arvensis.* We cannot take time to discuss these relations. (Compare Fig. 143.)

We will now pass from the forms of dehiscence to the mechanism of dehiscence. The important factor is the anatomical structure of the anther-wall (Fig. 153, *B*). The epidermis does not assist materially in the opening of the anther, the fibrous layer (x) (endothecium) is looked upon as the mechanically active tissue. As has already been stated, the weakest point is where the two valves are attached to the pillar of the connective. Thin-walled cells form the connecting tissue. The question arises, Whence the tension which causes the margins of the valves to separate from the connective? We can actually observe a shortening of the fibrous layer (in the mature anther) during gradual drying, so that the wall curls back. Let us consider the individual cell of the fibrous layer or endothecium. It is supplied on its *inner* wall and on the *radial walls*, as seen in cross-section, with thickened bands which project inward. The outer wall in contact with the epidermis does not contain these thickenings. These bands extend at right angles to the epidermis on the radial walls, those of the inner walls extend in all directions. The result of this thickening is that on drying the radial walls contract much more rapidly in the tangential direction than do the inner walls. The thickenings in the radial walls act as levers, exerting a force outwardly, but not inwardly. The tendency to shorten, which is manifest in the, radial walls, is neutralized as soon as the margins of the valves become separated from the pillar of the connective. The opening and recurving of the valves is a very sudden explosive act, whereby the pollen-grains are thrown out with considerable force. In the sporangium of ferns the weakest point corresponds to the group of thin-walled cells terminating the annulus. The latter is also the outermost cell-layer (see Fig. 128, *C*). The radial walls of the annulus lying parallel to the plane of the ring, as well as the outer walls, are thin; the remaining radial walls and the inner walls are thick. The cause for the immediate opening of the annulus (sporangium) is the same as in the anther, only that in the sporangium the evaporation of moisture is very rapid, since it can pass at once to the atmosphere through the thin outer walls of the cells.[1]

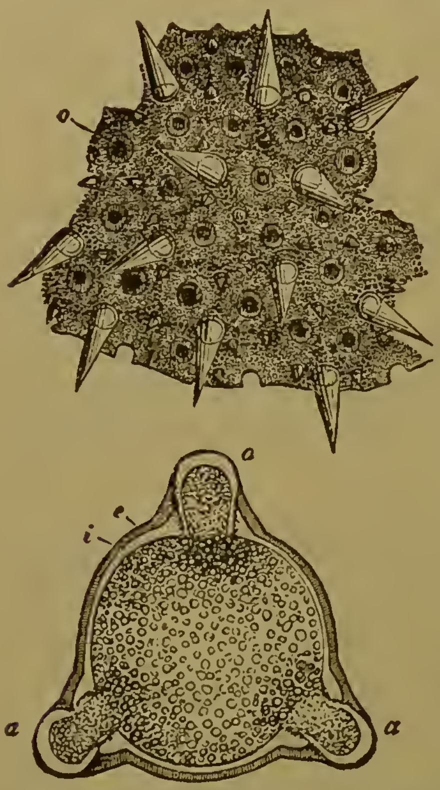

FIG. 154.—Pollen-grain of *Epilobium angustifolium*. (After Sachs.)

Returning to the structure of anthers, we must not forget to mention that in anthers which open by pores the fibrous layer is entirely absent, since they do not require any mechanism for opening (*Ericaceæ*, *Pirolaceæ*, *Melastomaceæ*).

The *pollen-grains* are isolated cells or small cell-bodies of spherical or oval form, with a *double* cell-membrane, the *intine* and

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[1] Among others MOHL, CHATIN, SCHINZ, PRANTL, and SCHRODT made special studies of this subject.

extine. The extine is firm and cuticularized; the intine is soft, and consists of cellulose. The latter enters into the formation of the pollen-tube. The points at which the pollen-tube formation is to begin are predetermined. The extine (Fig. 154, *e*) is supplied with one (monocotyledons), several, or many (dicotyledons) open or thin areas (*o*, *a*). In some cases there is a lid-like cover to these openings, which is removed when the pollen-tube begins to develop. The intine (*i*) is usually thickened at these thin areas (see Fig. 154). The protuberances and spines which sometimes occur on the extine may serve to attach the pollen to insects as well as to the stigma. The pollen-grains result from the quadrature of the pollen mother-cells, which are known as tetrads in the first stage. Fig. 155 represents an early stage of the pollen-forming anther-case. The cells immediately surrounding the pollen mother-cells, (*ep*) as well as a layer external to these, are subsequently dissolved. The cells (*ep*) are known as *tapetal* cells. Between the stage represented in the figure and the mature stage the young pollen-cells are found floating in the granular liquid which fills the entire anther-case. (Studied more in particular by NÄGELI, HOFMEISTER, and WARMING). The ripe pollen-grains usually form a powdery mass. Orchids offer a peculiar exception, the ripe pollen-grains of the entire anther remain united in a single mass, forming the *pollinium*. The teleology of the fertilization of orchids has been made a special study by DARWIN.

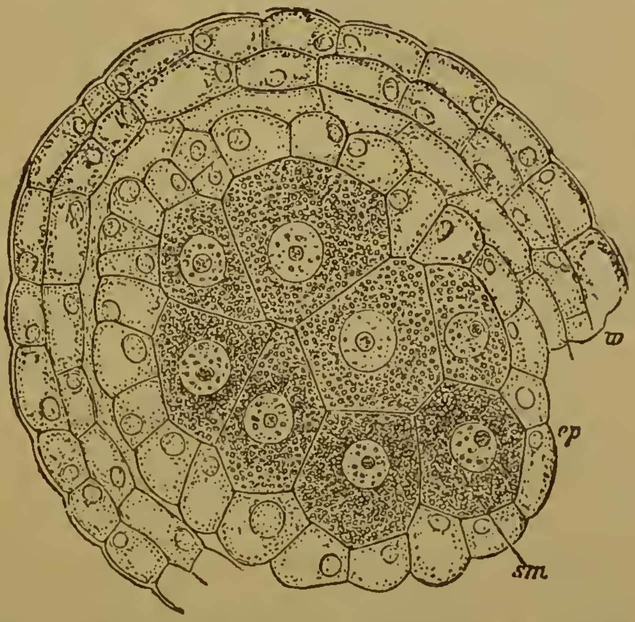

FIG. 155.—Cross-section through a young anther-case of *Funkia cordata*. *sm*, Pollen mother-cells; *ep*, tapetal layer; *w*, epidermis. (After Sachs.)

C. THE GYNŒCIUM. THE OVULE WITH THE EMBRYO-SAC BEFORE AND AFTER FERTILIZATION.

The gynœcium (pistil, according to the older terminology) bears the ovules (seed-buds) in the lower hollow portion, the ovary. The ovules are, as a rule, situated along the margins (*placentæ*) of the carpellary leaves or leaf. The number of carpellary leaves produces either a *monomerous* or a *polymerous* gynœcium. The polymerous gynœcium may either develop into a single ovary, when it is known as a *syncarpous* gynœcium; or each individual carpel may develop a pistil, the *polycarpous* or *apocarpous* gynœcium (*Ranunculaceæ*). Fig. 156 represents a cross-section of the polymerous syncarpous gynœcium of *Paris quadrifolia*; it is usually known as a "four-chambered ovary." Fig. 157 shows the polymerous syncarpous (*two-chambered*) gynœcium of *Atropa Belladonna*.

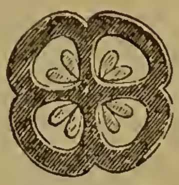

FIG. 156. — Cross-section through the ovary of *Paris quadrifolia*.
(After Krass and Landois.)

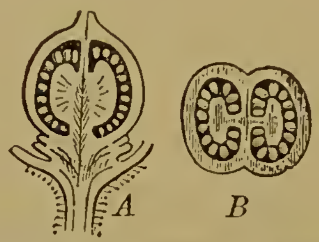

FIG. 157.—Ovary of *Atropa Belladonna*.
A, Longitudinal section; *B*, cross-section. (After Krass and Landois.)

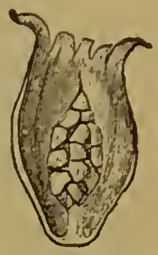

FIG. 158.—Central placenta of *Primula officinalis*, with the ovules removed.
(After Berthold and Landois.)

The manner in which the carpellary leaf-margins are united sometimes brings the margins nearly to the middle of the cavity of the ovary. This produces what is known as *axillary placentation* (Figs. 156 and 157), which is very common. More rarely the margins project little or not at all into the cavity of the ovary, when it is known as *parietl placentation* (*Violaceæ*). There are also intermediate forms of placentation which produce the incompletely many-chambered ovaries (*Papaver*). The so-called central placentation (for example, of the *Primulaceæ*; see Fig. 158) is not well understood from a morphological standpoint. It seems as though the floral axis (torus) produced the ovules. It is, however, possible that a caulome may develop ovaries.[1]

The Position and Form of Ovaries.—An ovule is said to be *atropous* (*orthotropous*) or *straight* when it forms a direct continuation with its stalklet or funiculus. The ovule is said to be *anatropous* when the funiculus extends along and is adherent to the

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[1] For fear that this statement may be misleading I will state that a caulome, *as such, will never produce ovaries.*—TRANS.

side of the ovule. The ovule is *campylotropous* or curved when its own body is more or less curved. An anatropous ovule is shown in the diagramatic figure of the angiospermous flower (Fig. 132); the two other forms are represented in the accompanying figure 159, (1 and 2). In the ovule, exclusive of funiculus, we distinguish the body of the ovule (*b*) with the embryo-sac (*c*) and one or two integuments; the latter (*d*, *f*) form the micropylar opening (*e*). The *hilum* is the point where the funiculus (*a*) is attached to the placenta; the *chalaza* (*h*) is the zone at the base of the ovule from which the tegumentary layers take their origin; the *raphe* (seam) is the line of union between the funiculus and ovule in anatropous ovules. In semianatropous (amphitropous) ovules the micropyle and chalaza are about equidistant from the hilum (see Fig. 159, 3). The anatropic and campylotropic ovules may further be *apotropous*, *epitropous*, or *pleurotropous*, according to whether the ovule is turned toward the base (apotropous), the apex (epitropous), or the side (pleurotropous) of the ovary. Such variations in position are intimately associated with the function of the pollen-tube.

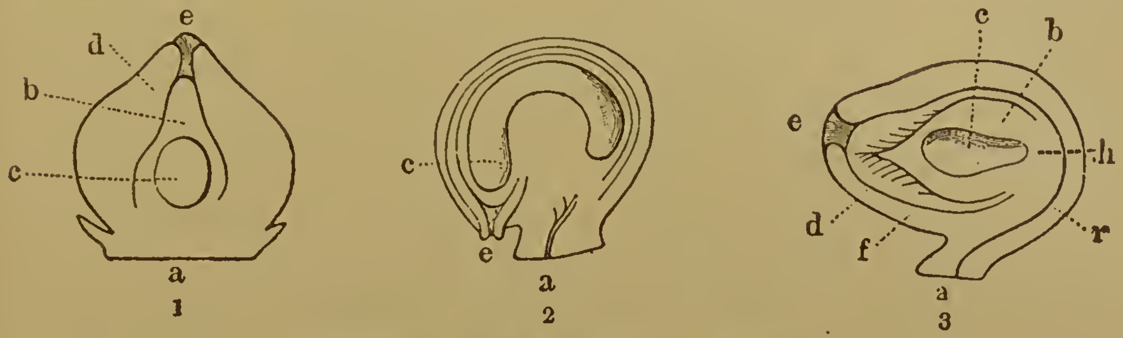

FIG. 159. (After Berthold and Landois.)

The Embryo-sac.—Immediately *before* fertilization the embryo-sac of angiosperms (monocotyledons and dicotyledons) contains, as a rule, three cells near the micropyle and frequently three cells at the opposite end. The latter have long been known as antipodal cells, but no particular function had been ascribed to them. According to more recent investigations, they very probably assist in the processes of nutrition. STRASBURGER's investigations gave us the most important results in regard to the nuclear divisions and fusions which result in the formation of the six cells mentioned and the secondary nucleus of the embryo-sac (see Fig. 132). One of the three cells near the micropyle takes up the rôle of the egg-cell. The other two, which are known as the *synergidæ*, are supposed to assist in the process of fertilization. From the observations made upon cryptogams it is assumed that among phanerogams the *nuclear substance* (nuclein) of the pollen-tube enters the embryo-sac and unites with the contents of the egg-cell. As a result the egg-cell begins to develop into the embryo. The literature on *embryology* is already very extensive. Special embryology has succeeded in explaining many of the observed phenomena and structures. The presence or absence of the suspensor, the behavior of the antipodes, the formation of nutritive substances *in* the embryo-sac (endosperm) as well as on the *outside* (perisperm), have already been explained, in part very clearly and in part only hypothetically. They evidently serve important functions in the processes of growth in the embryo as well as in the young seedling. For example, the suspensor, which is a simple cell-thread, assists in placing the embryo in that position within the embryo-sac at which the supply of nutrition is most favorable. According to TREUB's investigations, the suspensor of *Herminium Monorchis* has the power of forming protuberances along the placentæ. HOFMEISTER considered the endosperm as an enormously developed suspensor.[1]

In regard to the development of the embryo of *Capsella* (Fig. 160), it should be stated that among dicotyledons the embryo normally forms a depression at the stem-apex between the two cotyledons (*c*), while among the monocotyledons (*Alisma*) the elongated body of the embryo is a *lateral* development of the stem-apex instead of a terminal, as in the foregoing. Other variations also appear among monocotyledons: the originally terminal apex may later be crowded to one side by the cotyledon. Among dicotyledons there are also deviations from the *Capsella*-type of embryonal development.

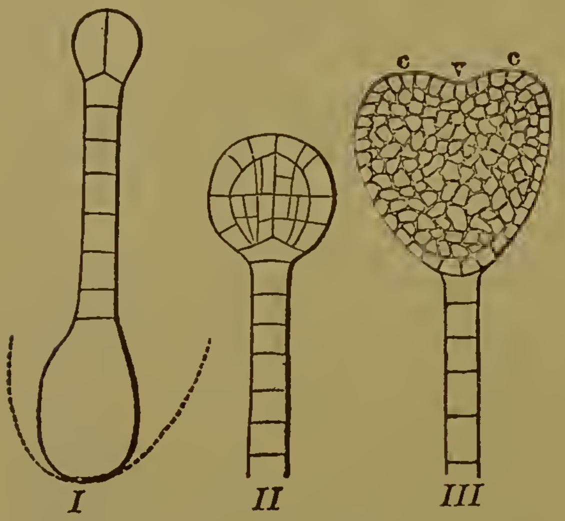

FIG. 160.—Successive stages in the development of a dicotyledonous plant, *Capsella bursa pastoris*. (Diagramatic.) The dotted line in *I* represents the wall of the embryo sac. The row of single cells represents the suspensor, *v* the apex of the future stem, *c* cotyledons.

The suspensor is finally removed and replaced by the developing root. Hanstein (following upon the investigations of Hofmeister) made a special study of embryonal development.

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[1] See also L. GUIGNARD, Ann. d. sc. nat., Sér. VI, T. XII, 1881.

The effects of fertilization are not limited to the gynœcium, but are manifest in the entire flower. Death and loss of organs which have served their function go hand in hand with new processes of growth which now serve new purposes. The petals, at times also the sepals, fall off; the stamens wither away. Frequently the floral axis (receptacle, torus) takes part in the fruit-formation, especially in epigynous flowers. Some of the *physiological* adaptations are as follows: structural arrangements to enable the seed and fruit to withstand the *period of rest*, to *distribute* them by *wind* and *insects*, and to insure a *favorable course during germination.* Some of these adaptations will again be referred to in the following chapters.

IV. THE MORPHOLOGY AND PHYSIOLOGY OF THE SEED AND FRUIT OF PHANEROGAMS.

A fruit in the strict botanical sense is the transformed gynœcium after fertilization.

From a *single* ovary results a *simple* fruit; from *several separate* ovaries of a flower is formed the *aggregate* fruit. From one flower we have a *single* fruit; from an inflorescence we get the *multiple* or *collective* fruit (*Ananas*, multiple fruit; cherry, simple and single fruit; *Ranunculus*, aggregate fruit).

Other parts of the flower besides the gynœcium may take part in the formation of the fruit and form false fruits in distinction to the true fruits defined above. Example: the *receptacle* of the strawberry becomes fleshy and apparently represents the main axis of the false fruit; it is also an *aggregate* fruit, since many separate ovaries (akenes) are situated upon the pulpy receptacle. The apple is also a false fruit, since the hollow floral axis (*cupula*) takes part in its formation. The pappus-like developments on the fruits of *Compositæ* are modifications of the calyx.

Single fruits may be divided into five kinds: 1, *capsule;* 2, *carpels;* 3, *achenium* (*akene*); 4, *drupe;* 5, *berry.* (See figures on p. 234.)

1. The capsules open at maturity according to a fixed method. They may be subdivided as follows.

(*a*) The *legume* or true pod is a single-chambered fruit formed from one carpel; seeds are placed along the ventral suture; dehiscence along the dorsal and ventral suture from above downward (*Leguminosæ*).

(*b*) The *follicle* opens along the ventral suture only (*Pæonia*).

(*c*) The *silique*, two-chambered; dehisces along both sutures from below upward; the placentæ, as the partition, remain behind while the valves fall away (*Cruciferæ*).

(*d*) True *capsules*, usually dehisce from the apex downward, or they may discharge the ovules through chinks or pores, as in *Papaver;* they may open at the teeth-like projections near the apex, as in *Primula;* by valves opening lengthwise, as in *Iris* and *Syringa*; or transversely, as in *Colchicum autumnale;* or by the dissolving of the partition, as in *Datura.* We may therefore recognize loculicidal, septicidal, and septifragal dehiscence.

2. *Carpels* (splitting fruits) are again divided into:

(*a*) *Cremocarp*, consisting of a pair of akene-like ovaries completely united in the blossom, but splitting apart when mature (*Umbelliferæ*).

(*b*) *Loment* resembles a legume, but splits up crosswise at distinct joints or transverse septa (*Desmodium*).

The *achenium*, *drupe* (stone-fruit), and *berry* do not open according to such systematic methods.

3. The *achenium* is usually small with a dry woody coat. This fruit may again be divided into: (*a*) *achenium* proper, (*b*) *caryopsis*. In both the seed is closely united with the seed-covering or pericarp. The achenium arises from inferior ovaries (*Compositæ*), the caryopsis from superior ovaries. (*c*) *Samara* or *key-fruit*, which is an akene furnished with wing-like appendages (elm, ash, maple). (*d*) Nut; this as well as the key-fruit has *free* seeds lying within the seed-covering. The covering of the nut consists of typical sclerenchyma cells (hazelnut, chestnut, acorn, etc.).

4. *Drupe* (stone-berry). The inner layer of the fruit-covering (*endocarp*) is very hard; the outer layer (including mesocarp and epicarp) is succulent and much enlarged, as in our stone-fruits, the cherry, plum, etc.; or it may be dry and fibrous, as in the cocoanut; or almost leathery, as in the walnut and almond. (The entire fruit-covering is usually known as the pericarp.) The

apple-fruit (pome) may be considered as a stone-berry with a thin pergament-like endocarp (RADLKOFER, WARMING).

5. *Berries.* The entire pericarp is soft and fleshy, or leathery at the outer part (grape, tomato, orange).

(The foregoing description of fruit-forms is according to THOMÉ.)

There are many structural arrangements to facilitate the distribution of seeds and fruits. Although the physiological factors were not considered in the description of fruit-forms, we must not for a moment forget that such factors nevertheless exist, some of which have been carefully worked out, while others require further elucidation. In 1873 HILDEBRAND published his communication on the Distribution of Seeds by Plants, to which I refer the student, and from which the following statements are taken.

The following peculiarities of seeds and fruits facilitate their distribution by air-currents.

1. Reduced size of seeds (including the spores of cryptogams); lightness of seeds (orchids).

2. Flat form of seeds (*Lilium*, *Tulipa*); wing-like appendages (conifers, many crucifers).

3. Wing-like appendages of fruits (*Ulmus*, *Fraxinus*, *Betula*, *Acer*, *Rheum*, *Isatis*); the winged appendages may also be formed by modified bracts (linden, hawthorn), or by the perianth (*Salsola*).

4. Hair-like appendages to seeds (*Epilobium*, *Salix*, *Gossypium*).

5. Hair-like and feather-like appendages to fruits (*Anemone*, *Compositæ*).

(The following figures will assist in explaining fruit-forms as well as the appendages just referred to.)

We must also mention the *arillus* or *seed-mantle* with which many seeds are equipped. It may develop from the funiculus, the hilum, or the micropyle. In the seeds of *Evonymus europæa* it is of a yellowish-red color; in seeds of *Taxus* it is well developed and red in color. Such highly colored formations attract animals, especially birds, which feed upon the seed. Other structural arrangements for the successful distribution of seeds are the thick and hard seed-coverings (*testa*), which resist the digestive action of the juices of the stomach and intestines of animals. Animals,

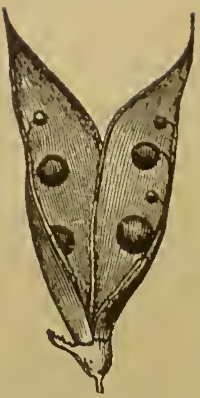

FIG. 161.—Pod.
(After Berthold and Landois.)

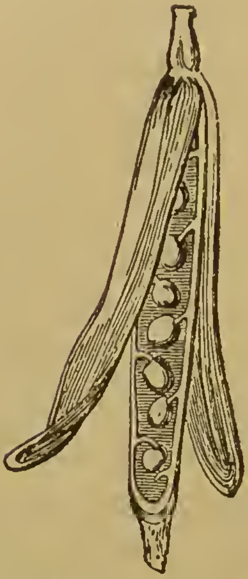

FIG. 162.—Pod of *Brassica Napus*.
(After Krass and Landois.)

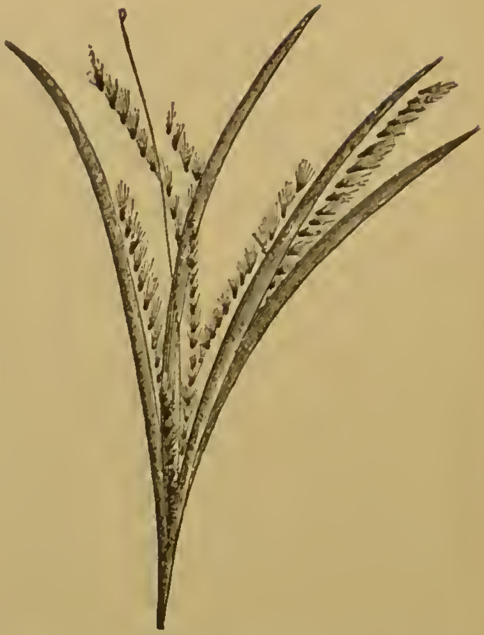

FIG. 163.—Seed-capsule (open) of *Epilobium augustifolium*. Tufted seeds. (After Berthold and Landois.)

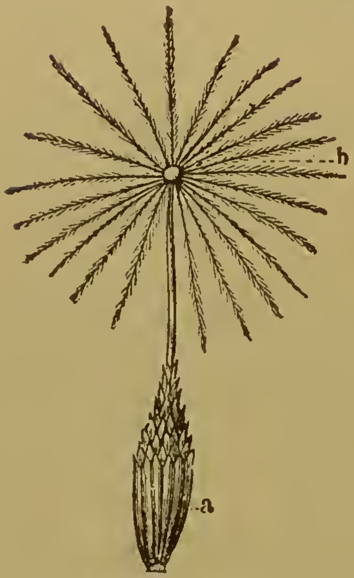

FIG. 164.—Achenium (*a*) with parachute-like arrangement of the "pappus (*b*)." *Taraxicum officinale*.
(After Berthold and Landois.)

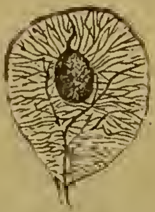

FIG. 165.—Winged fruit of the elm.
(After Berthold and Landois.)

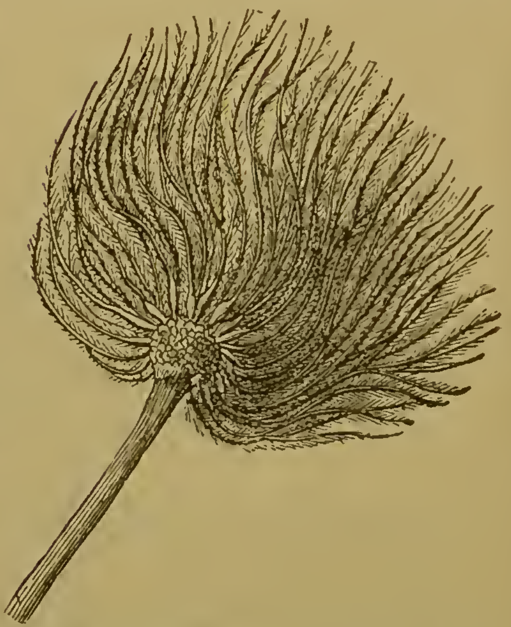

FIG. 166.—Akenes of *Anemone pulsatilla* with the long hair-like styles.
(After Berthold and Landois.)

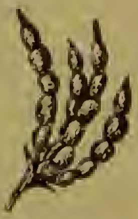

FIG. 167.—Pods of *Ornithopus*.
(After Berthold and Landois.)

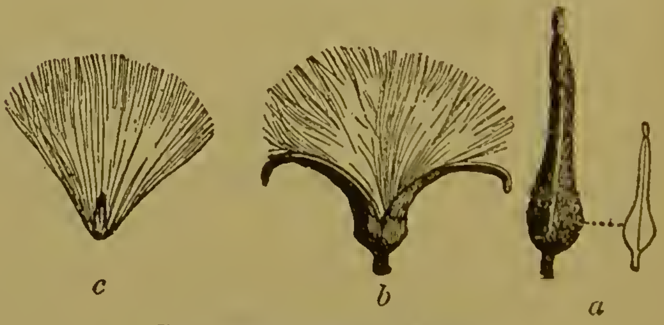

FIG. 168.—*Salix Caprea*.
a and *b*, Fruit; *c*, seed. (After Krass and Landois.)

especially birds, may carry these seeds great distances on land or across the water.

In some cases the arillus has an entirely different function. Among *Leguminosæ* it forms a *scission tissue* between the placenta and the seed, causing delicate tissues to rupture. In *Nymphæa* the arillus serves to keep the seed afloat. The seed floats upon the surface of the water for about forty-eight hours, so long as there is air in the cavity of the arillus; as soon as water displaces the air the seed takes a position with its apex upward and falls out of the sac to the bottom of the water, where it begins to germinate. In various families (*Berberidaceæ*, *Turneraceæ*) the arillus serves the same function as the winged appendages of seeds.[1]

Leaving out of consideration the arillus, which is not always present, we have yet to discuss the *seed-coat.*[2] Sometimes we may distinguish two layers, an inner (*tegmen*) and an outer (*testa*), which, however do not always originate as two separate coats (Radlkofer). The above-mentioned winged and hair-like appendages are products of the seed-coats. In some seeds there are still other hair-like appendages which serve to attach the seed to the soil during germination.[3] This is also the case in some fruits. The mucilaginous cell-walls of the outer seed-coat serve a similar purpose, as in *Linum usisatissimum*, *Cruciferæ*, *Labiatæ*. The mucilage also retards the evaporation of moisture from the seed (Klebs).

The endosperm, which we have already learned to know, needs to be considered more from a physiological standpoint, especially in connection with the discussion of seed- and fruit-coats. Communications and citations of literature in regard to this subject are found with Marloth.[4] In 1890 W. Hirsch published a communication on The Adaptive Arrangements of the Storage-tissue of Seeds.

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[1] Planchon, Baillon, Hildebrand, Bachmann, Pfeiffer, and others, from whom we have taken the foregoing statements, made special studies of this subject.

[2] See Pfeffer's Untersuchungen a. d. Botanischen Institut zu Tübingen. Frank gives numerous citations to the literature of this subject in his Lehrbuch der Botanik, p. 159 (1892). See also R. Loose, Die Bedeutung der Frucht und Samenschale, etc., Berlin, 1891.

[3] Grütter, W., Über den Bau und die Entwickelung der Samenschalen einiger Lythrarieen, Bot. Zeitung, 1893.—Trans.

[4] Über mechanische Schutzmittel der Samen, etc., Botanische Jahrbücher IV, 1883.

The chief function of the seed-coat is purely mechanical, forming a protection against radial pressure. Seeds must be protected against injury during their transport to the places of germination; they must also be protected during their rest in the soil against the attacks of animals. Protection against evaporation usually goes hand in hand with mechanical protection. The fact that the formation of thick-walled mechanically active cells may take place not only in the seed- or fruit-coats, but also in the seed-albumen (endosperm), is highly interesting. Much requires further investigation, but we are enabled at present to arrange the following "biological" groups of plants: 1. The seed-coat consists of thin-walled cells and encloses the thick-walled albumen of the seedling: *Colchicum*, *Viscum*, *Plantago*, *Arum*, *Rubiaceæ*. 2. Thick-walled cells of the seed-coat and thin-walled endosperm: *Syringa*, *Saxifragaceæ*, *Helleborus*, *Papaver*, *Glaux*, *Hippophæ*, *Giamineæ*. (After MARLOTH.) (Compare Figs. 91 and 169.)

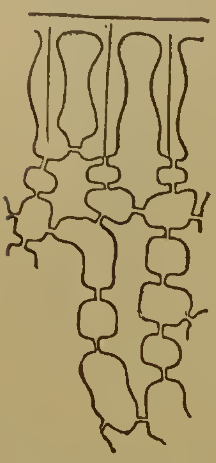
FIG. 169. — Peripheral cross-section of a portion of the endosperm of *Polygonatum vulgare*. (After Haberlandt.)

In still other cases both the seed-coat and the endosperm take part in forming the mechanical tissue. PFITZER[1] made some very interesting observations in regard to the adaptations for the germination of seeds with hard fruit-coats, as those of the *Palmæ*. Based upon his communication I will state that among the *Borassinæ* the points for the escape of the seedling are preformed. The thinnest part of the fruit-coat is immediately in front of the embryo. In *Cocos* there is a valve at the point of germination which is readily removed. This valve or opening corresponds in position to the style. Pfitzer also found special arrangements for holding the *endosperm* of the ripe fruit so that the seedling must retain its proper position in regard to the germinal opening, as, for example, conical projections from the seed-coat into the endosperm-substance.

On pp. 142, 143 we have explained more or less clearly that the seedlings of *Cruciferæ* and *Papilionaceæ*, which are without endosperm, present physiologically similar structures in the much-thickened cotyledons (rich in oil).

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[1] Ber. d. Deutsch. Bot. Ges., 1885.

We will not enter into a discussion of the arrangements for the ejection of seeds from the ovaries and fruits. We will only mention a peculiarity of the seeds of *Erodium*, namely, under favorable circumstances they are forced into the ground by the movements of the hygroscopic awn. In *Arachis hypogæa* (peanut) the basis of the ovary grows downward, carrying the young ovary into the soil, where it matures. Some of the mechanical movements will be more fully explained in the chapter on the phenomena of movements.

GERMINATION.

Germination takes place after the period of rest, provided there is sufficient *moisture*, a *temperature* varying, as a rule, from 6° C. to 45° C. (SACHS), and *air* (O). Light is therefore not necessary. The appropriation of oxygen will be discussed later.

The *duration of the viability* of seeds is limited, but differs greatly in different plants. Some seeds must be placed in the soil at once (coffee), many others can germinate at once or later; some remain viable only during one vegetative pause (winter); others several or many years. The reports that seeds one thousand or two thousand years old were still capable of germination, are questionable. Many seeds can *not* germinate immediately after their separation from the mother-plant. According to SACHS, potatoes and onions cannot send out shoots during November or December of the same season in which they were formed.

The subject of the "rest-period" of seeds as well as "rest" in general (tubers, bulbs, buds rest also) is more difficult of explanation than one would suppose. The following statement is according to the authority of SACHS[1]: We may assume that seeds, bulbs, etc., which are capable of germinating at once receive the necessary amount of *ferment* during their formation while still connected with the mother-plant; in other cases a longer period (and perhaps lower temperature) is required to form the necessary ferment. These ferments (as, for example, the starch-dissolving *dias-*

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[1] Vorlesungen, p. 425.

tase) must be present in order that the reserve materials may be dissolved, since they cannot be utilized in the processes of nutrition while in the solid state.

In regard to the "annual vegetative period," we soon recognize that this phenomenon needs further elucidation (PFEFFER).[1] According to my opinion, the investigation of the properties and peculiarities of organisms reveal *relations* and *adaptations* which we can recognize as such without being able to explain them. Let us consider a few examples. 1. We can see that the *annual periodicity* is not peculiar to all plants; the regularly recurring period of rest seems to be a "facultative" property of many plants which manifests itself when desirable. 2. We can also see that definite plant-forms are adapted to definite external relations.

Ad 1. Many tropical plants while in their natural home develop leaves and flowers during the entire year. If, however, an annual dry period sets in, as is very common in tropical regions, we notice that such plants undergo a periodic rest, corresponding to the dry seasons.

Ad 2. Climatic adaptability will have reached its limit when palms can survive in our climate without artificial protection. Our native oak and beech can exist in Madeira, but will shed their leaves in spite of the moist, mild climate. The cherry is evergreen in Ceylon, but does not develop fruit (DE CANDOLLE). According to HUMBOLDT, the grape of Venezuela bears leaves and fruit during the entire year. HARNIER noticed the same thing in the grapes of central Africa (Khartoum).

V. THE GENERAL PHYSIOLOGY OF REPRODUCTION.

In this chapter the statements are based essentially upon the investigations of NÄGELI and in part upon those of SACHS, unless other citations are given.

A. AGENTS IN FERTILIZATION. CROSS-POLLINATION. SELF-POLLINATION.

PFEFFER'S recent investigations have revealed the cause which induces the free-swimming spermatozoids of cryptogams to move toward the archegonia. It is a *chemical agent.* Among ferns it is malic acid, among leafy mosses it is cane-sugar, which acts as the peculiar stimulus that attracts the spermatozoids to the opening of the archegonium. Among phanerogams the pollen-grains are transferred to the stigma (or micropyle) by means of insects or the wind. Plants dependent upon the wind for pollination are said to be *anemophilous;* those dependent upon insects are *entomophilous.* In some plants pollination is dependent upon water-currents; they are said to be *hydrophilous.*

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[1] Pflanzenphysiologie, II, 106.

The great majority of phanerogamic flowers are structurally adapted to be fertilized by *other* flowers of the same species; they are open at the appropriate time: *chasmogamous* flowers. There is also a small group of plants dependent upon self-fertilization and whose flowers therefore remain closed: *cleistogamous* flowers. Example: *Ranunculus aquatilis.*

A study of these relations gives us an insight into a large number of adaptive arrangements. Some of the subsequent statements are repetitions, but will not be amiss, because of the importance of the subject. The anemophilous plants have inconspicuous flowers of dull colors and very numerous pollen-grains; they sometimes bloom before the appearance of the leaves. Examples: *Gymnospermæ* and *Gramineæ.* In the former (*Pinus*) the pollen-grain may have winged appendages. The entomophilous flowers require and possess large showy flowers, with odor and nectaries for the purpose of attracting insects.

From the frequent occurrence of hermaphroditic flowers among phanerogams it must not be concluded that self-pollination is the rule. The majority of hermaphroditic flowers as well as flowers in general are specially adapted for the process of cross-pollination. Of such adaptations the three following may be mentioned without considering the mechanical structures thereby involved. 1 and 3 refer to hermaphroditic flowers.

1. *Dichogamy.* The andrœcium and gynœcium of the same flower do not mature at the same time. If the anthers mature first, it is known as *protandry* (*Compositæ*); if the pistil matures first, it is known as *protogyny* (as in *Plantago media*). Though cross-pollination is the rule, hermaphroditism is not an unsuitable arrangement; by it is represented the largest possible number of flowers of both sexes with the least expenditure of substance.

Furthermore, it is clear that since the visit of insects depends upon the existing plan of organization it also guarantees the greatest success.

2. *Dicliny.* It is either *monœcious*, that is, male and female flowers occur upon the same plant (example: *Zea Mays*), or *diœcious*, if the sexes occur upon different plants (examples: *Salix*, *Coniferæ*).

3. *Heterostyly.* In plants of the same species (examples: *Primulaceæ*, *Lythrum Salicaria*) there may be two or three sets of stamens differing in length (*dimorphism*, *trimorphism*); corresponding to these stamens, the pistils are also of different lengths. The following is the principle underlying this arrangement. That part of the body of the insect which comes in contact with the stamens of the length *a* of one flower also comes in contact with the stigma of the same length of another flower. The above method of pollination produces the best results, as has been verified by control experiments. It has also been observed that in flowers with elements of unequal length the female flowers are more or less sterile. *In-and-in breeding* (Inzucht) is the term applied to that form of reproduction which occurs in the same plant-forms, in distinction to hybridization (crossing). We also know that the most common form of crossing is by two different individuals of the same species (cross-fertilization in the narrower sense), the special organization of which we have just learned to know. There are, however, certain plants with flowers especially adapted for *self-pollination* (Hermann Müller made a special study of this adaptation). Many land-plants open their flowers only partially or not at all on rainy days (*Veronica hederæfolia*, *Drosera rotundifolia*); the submerged flowers of water-plants also remain closed, and pollination takes place in the small air-space between the floral coverings.[1] Example: *Ranunculus aquatilis*. Such *cleistogamous* flowers develop much less pollen than the *chasmogamous* flowers, which are dependent upon wind and insects for pollination. The cleistogamous flower of *Viola nana* forms about 100 pollen-grains, while an entomophilous flower of *Leontodon* forms about 243,600.

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[1] Schenk, Biologie der Wassergewächse.

B. FERTILE SEEDS. HYBRIDIZATION. APOGAMY.

In regard to the production of fertile seeds, the following factors are of prime importance.

I. Only one pollen-tube is engaged in fertilizing an ovule. If pollen-grains from different species of plants fall upon the same stigma, only that one will be active in fertilization which has the greatest sexual affinity (see II). According to recent investigations, it is necessary that some of the nuclear substance of the pollen-tube (*male pronucleus*) fuses with the nuclear substance of the egg-cell (*female pronucleus*). The manner in which the pollen-tube reaches the egg-cell has already been described.

II. We must distinguish between *systematic* and *sexual* relationship; they are not identical. The latter may be ascertained by methods of crossing; the former we judge by the similar or dissimilar characteristics. Plant-forms which are widely separate systematically are often closely related sexually, that is, they can be crossed; as, for example, *Lychnis diurna* and *Lychnis flos cuculi;* while *Pirus malus* and *Pirus communis* (apple and pear) show only slight sexual affinity or perhaps not any. Species of *Dianthus* are readily crossed; species of *Silene* with difficulty or not at all; *Rosaceæ*, *Salicaceæ* with comparative ease; *Papilionaceæ* with difficulty; etc. It is further interesting to note that while *a* may be fertilized by *b*, *b* will not be fertilized by *a* (non-reciprocal or imperfectly reciprocal hybridization). Different varieties cross very readily (*variety-hybrids*), different species less readily (*species-hybrids*), different genera very rarely (*genus-hybrids*). The following statement is generally applicable: *Only such plant-forms as show a close systematic relationship can be successfully crossed.* This does not preclude the possibility that the fertilization between varieties may be more effective than fertilization between two individuals of the same variety.

III. Fertility and other conditions of hybridization. The sexually produced offspring of two plant-individuals which do not belong to the same systematic unity, but to *different* varieties, species, or genera, are called *hybrids* (*bastards*). The greater the difference in the systematic affinity of the parents of a hybrid the greater the liability to sterility. Widely separate species do not form hybrids; slightly related species may form a sterile hybrid. (The hybrid between the apple and pear would be sterile.) Closely related species will form hybrids with limited fertility, at least they are less fertile than the parental forms. *Vegetatively* the hybrids are often much stronger than the parental forms; they "luxuriate."

IV. According to NÄGELI, the male and female hereditary qualities are about equally transmitted in the hybrid. This, however, does not imply that the hybrid *AB* (resulting from the fertilization of *A* by *B*, presents the same peculiarities as the hybrid *BA*. Nägeli maintains, however, that the hybrid can have no properties or peculiarities not contained in the ancestral forms, nor can there be anything lost which is contained in the ancestral forms. Peculiarities may lie *dormant* and become entirely lost, or may develop later (*reversion*, *atavism*). Such latent qualities do not develop when varieties of cultivated plants are propagated asexually; by this means the race or species may be kept almost unchanged and it is extensively utilized by horticulturists in propagating desirable fruits and flowers. Propagating from the seeds of such races shows "degeneration;" that is, their *latent* qualities develop (NÄGELI). A hybrid *AB* which resembles *A* more nearly than *B* will revert more rapidly to the parental form *A* if continually fertilized by *A* than into the parental form *B* by continuous fertilization by *B*.

V. There are also "derived" hybrids. They result when one hybrid and one of its parental forms, or some other parental form or hybrid, unite sexually. There are also cases in which four or more varieties or species may be represented by one hybrid. MILLARDET's [1] experiments with the *grape* have enabled us to make great practical use of hybridization. In North America there are a number of wild-growing species of *Vitis* which can be crossed. Of our European *Vitis vinifera* not a single variety is proof against the attacks of the grape-louse (*Phylloxera*). According to Millardet, a hybrid formed by crossing different American species with the European species produces a grape which will, to a certain extent, resist the attacks of *Phylloxera* and various destructive fungi.

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[1] See SACHS' Vorlesungen, p. 961.

VI. Finally, we will briefly mention the rare occurrence of "apogamy" and related phenomena (DE BARY and his pupil FARLOW). It has been observed that among some ferns a plant will develop from the prothallium without fertilization, hence asexually (budding). According to A. BRAUN (1856), the egg-cell of *Chara crinita* may develop into an embryo without being fertilized. The egg-cell of the euphorbiaceous genus *Cœlebogyne* will also develop by budding. Only the female plant occurs in Europe.

C. VARIABILITY. CONSTANCY. HEREDITY.

The properties of a plant *as a whole* may be separated into those which are *constant* and those which are *variable.* Constancy and variability are clear conceptions, but their application in regard to heredity, sex, and environment soon bring to light great difficulties.

Constancy is the result of heredity acting from one generation to another; the influence of both parent-plants upon the daughter-plant. Variability is shown in slight differences between the daughter-plants among themselves and in the differences between daughter-plants and parents. (According to Nägeli, heredity and variability are almost inseparable; variability depends on heredity.)

To us variability and constancy (hence also heredity) are properties *given* to living created beings. There is no satisfactory scientific definition for heredity.

The following statements are in accordance with our present knowledge of variability. There is a variability due to *external* causes, such as the influence of the surrounding medium, climatic conditions, etc.; and a variation due to *internal* causes which cannot be perceived externally. The latter causes are least understood. The external causes can only be interpreted teleologically; we are unable to give them an *ultimate* causal explanation. We will cite an example of variation due to external causes. *Polygonum amphibium* usually grows near the margins of ponds, but may also occur on dry land. It has been observed that the anatomical structure of the land-form is different from that growing in water. In the former the intercellular aerating system is slightly developed, while the vascular system is strongly developed. In the water-form the reverse is true; the air-chambers are large, which insures a supply of air and facilitates floating; the vessels are less numerous than in the land-form. This shows that there is a suitable adaptability between the external environment and the anatomical structure. Physiology is, however, unable to explain these causal relations. It cannot explain why a locality deficient in water will decrease the intercellular spaces and increase the vascular bundles. We can, however, understand somewhat the suitableness of such adaptation. If we recognize such knowledge as an *explanation of the cause*, we make an inexact use of the expression, since we presuppose something as known which is unknown.[1] Below we will have more to say about the variation of plant-forms and the effectiveness of external and internal causes. We will conclude this chapter with a remark on *constancy*.

Nägeli[2] makes a sharp distinction between *constancy in the narrower sense* (*constancy in time*) and *permanence* (*constancy in space*). What we usually call "constancy" can generally only have reference to space. We compare individuals developed at the same time in different localities. Constancy in time (real constancy) is usually not tested by the systematist. This would be done by securing the same species or varieties from *different* localities and cultivating them *for years* under the same environment.

We will now discuss the differences between the theory of special creation and the theory of natural descent.

D. Special Creation and the So-called Theory of Natural Descent.

The doctrine that the first plant-forms sprang from lifeless matter at the command of the Creator, hence were formed in a supernatural way, is in no wise contradictory to the teachings of natural history. We learn from the book of Genesis (1) *that a series of different plant-species* were created, (2) that the "earth," hence lifeless matter, brought forth the plants.[3] Chemistry teaches, in fact, that the plant-bodies do not contain any other elements than those which are found in lifeless matter. Whether dead substances are capable of bringing forth simple vegetable organisms at the present time is of no great consequence. Science at present denies any such origin of simple organisms, since all experimentation is in support of such a denial. This is to be especially emphasized, because it is generally believed that to assume the aid of a supernatural agency in forming living organisms from dead matter is unscientific. In regard to higher plants, the agreement is universal that there is no origin *de novo.* This being the case, the question for discussion is, Where do the *higher* vegetable organisms come from? Are they specially created, or have they descended in a natural way from pre-existing lower forms?

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[1] In connection with this statement it might be well to remind the student who is inclined toward speculative reasoning that *all knowledge*, no matter what it may be, is based upon something which is *unknown*, and which is therefore taken for granted.—Trans.

[2] Mech.-physiolog. Theorie der Abstammungslehre. 1884.

[3] It is a questionable proceedure for a modern scientist to quote the writings

Let us test the theory of natural descent, which teaches that *all* plants have the same phylogenetic origin and firmly denies any supernatural creation either now or in the past. We will present and criticise the views of one of its strongest advocates, namely, NÄGELI.

According to Nägeli, nothing is permanently fixed or unchangeable—neither the variety, nor the species, nor the genus, family, order, nor class, etc. The variety shows a certain constancy, leaving out of consideration the "modifications due to locality;" a greater constancy is noticeable in the species; the genus is still more constant; and so on up. We maintain that a number of forms or types, which need not correspond with any species of our present classification, were *created;* it is impossible to say whether these created and, *to a certain extent*, variable forms corresponded in the one case to a species, in another to a genus, or perhaps to a still more comprehensive group. The strong point in our position lies in the fact that, since variability is not without limitations, the *constancy in time is absolute or real.*

Empiricism is again in *our* favor, more so than casual observation would indicate. The question is, How do new species originate? According to NÄGELI's own statements,[1] it must be admitted that *observation and experiment have not demonstrated the origin of a species, neither due to internal causes* (idioplasm)

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of the ancient Hebrews in support of his theory. They certainly are not authority on scientific subjects.—TRANS.

[1] See ref. 2 on p. 244.

nor to external causes (influence of nutrition, light, temperature, mechanical stimuli, etc.). Nägeli's theory also differs from empiricism in regard to what external and internal causes can produce. In one important point we agree with Nägeli; that is, as to the influence of nutrition. This factor is plainly under the control of direct observation.

"No inherited property, no variety, race, or species, owes its origin to nutritive processes." It is important to bear in mind that the same varieties may occur in localities widely different, and that two slightly different varieties may occur in the same locality. Years ago Nägeli also pointed out the following general phenomenon. Mountain-plants transplanted to the valley lose their mountain habits, although they evidently lived among the mountains for thousands of years. Climatic influence therefore does not produce constancy.

Nägeli assumes that the "stimuli"[1] resulting from *internal* and *external* causes are active in producing new species, genera, etc. The *internal causes* are supposed to lie in the hidden nature and structure of *idioplasm.* These causes produce a continual progressive change in the micellar structure of the idioplasm, causing it to become more and more complicated and highly organized (principle of perfecting); primarily, all hereditary transformations due to external causes are the result of idioplasmic changes. *Progressive organization* and *division of labor* are in general induced by internal causes; while the *specific constitution* and variation in form, organization, and division of labor, the adaptation to the external environment, are the result of *external* causes (stimuli). Nägeli's theory differs from that of Darwin. According to the latter, the external causes act negatively in repressing or stamping out that which is not suited or adaptable (*natural selection* with *struggle for existence*). According to Nägeli, the external stimuli act mechanically upon the micellar structure of the idioplasm[2] to produce the adaptive changes. (Further differences in the theories of Nägeli and Darwin will be given below.)

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[1] By "stimuli" Nageli means those influences upon the plant-organism which induce reactionary effects, as mechanical stimuli, light, warmth, cold. In Nägeli's Abstammungslehre, p. 102, there occurs a contradictory statement: most climatic influences are classified with the indifferent influences, while on the above page warmth and cold are classed among the effective stimuli which aid in forming hereditary qualities.

[2] Abstammungslehre, p. 139.

Nägeli does not deny that we do not know *how* the stimuli act upon the idioplasm to produce the required adaptive changes. But the desire to formulate a theory of natural descent induced him to supply the necessary connecting links from fantasy. For example, he tries to explain in what manner the mechanical tissue-system was in all probability formed. Let us follow his argument. He says that " tensions of pressure and of pulling are strongest where the mechanical cells actually occur." Further, " tensions must predominate in the elongated cells of the fibro-vascular bundles, because the short parenchyma cells with their large intercellular spaces cannot so readily resist these tensions, and would become displaced." The question now arises, Why are ring-vessels, bast, and various cell-wall thickenings formed? According to Haberlandt and Ambronn, the mechanical tissue with the vascular bundles is not always formed from a common cambium. The *well-established* teaching of Schwendener, that the mechanical system is independent of other systems in its arrangement and position, does not harmonize with Nägeli's conception. It is also well known that the mechanical elements of the grass-internodes develop at the periphery, *although* they are protected against stimuli of tensions by the leaf-sheath. Further, in organs subject to bending, tensions are greatest at the periphery. According to Nägeli, water-plants are evolved from or converted into land-plants. Typical water-plants have a *central* bundle of elongated elements. Before they can be changed into land-plants it is necessary for them to develop peripheral elongated elements. Is it probable that the mutual adaptation and arrangement of mechanical and assimilating systems is due to blind mechanical forces? Can any physiologist understand the complication which arises when there is established an harmonious, rational equilibrium between the position of mechanical and assimilating tissues at the points of maximum tension and of favorable illumination? This much is certain, that the mechanical-physiological theory of descent can here be no longer applied.

Although Nägeli has allowed himself to be blinded by his love for the theory of the natural origin of plants, yet his acute critical powers are manifested in his attack on Darwin's theory of natural selection. Darwin's theory of *selection* and Nägeli's theory of *descent*, which he himself has designated as the *theory of direct cause*, have one thing in common. It is, that the present condition of the organic kingdom was brought about by individual *variations* and the survival of the fittest in the struggle for existence.

(Competition or the struggle for existence in both the plant and animal world is, according to our opinion, a fact, caused on the one hand by the excessive productiveness of the created organisms and on the other by the constancy of the available area of the earth's surface. This competition is further necessary in establishing a beneficent equilibrium in nature.)

In Darwin's theory of selection, *erratic variation* is the *propelling* factor, *selection* is the *progressing* and *ordering* factor. According to Nägeli's theory, *variation* is both the *propelling* and *progressing* factor. *Selection*—that is, the survival of the individuals best adapted to the environment—is, according to Darwin, the chief means of evolution or perfection ; according to Nägeli, competition is wholly without influence toward advancing from a lower to a higher ; it only removes that which is less capable of existing. According to this author, an alga would have been converted into an oak, an amœba into a mammal, even without competition ; only there would be in addition all the descendants which have gone out of existence as the result of competition.

So much concerning the difference between these two theories. We shall now give some of Nägeli's objections to Darwin's theory of selection which we believe to be important.

1. The undetermined effects of undetermined causes presents so much which is accidental that this *erratic* variation in selection cannot be harmonized with scientific thought.

2. The crosses of varieties due to natural causes are different from those of artificially produced varieties. Natural varieties fuse or cross with difficulty, and are not changed by such a process.

3. Useful variations appear only when the variations have advanced to a considerable degree and have affected a large number of individuals, thus enabling them to crowd out competitors. But since variations must continue for a long time on a small scale, and can exist only in a few individuals during that time, it is evident that a struggle for existence and natural selection cannot come into play. The following is an example given by Nägeli : the progenitors of our ruminants were hornless; due to variation, a few of them developed microscopic horns. Since within the first fifty or more generations these horns must have been functionless on

account of their minuteness, we cannot speak of a selection and a "struggle." Furthermore, crossing would continually tend to remove the incipient variation.

4. Nutritive influences do not produce hereditary changes.

5. According to Darwin's theory of selection, the more useful a property of an organism is the more constant it must show itself in the process of selection; structures which do not prove advantageous must be variable. It has been observed, however, that in the plant kingdom the laws of cell-division and other morphological characters are the ones which prove to be exceedingly constant; these certainly have nothing to do with selection. Here Nägeli also includes phyllotaxy (to be discussed later).

Space will not permit us to enter into a fuller discussion of Darwin's theory and Nägeli's objections thereto.

Although Nägeli calls his theory the "theory of direct cause," it does not assist in elucidating matters when he assumes that it is the *unknown structure and mechanism* of the idioplasm which causes the evolution of the organic world. With such total obscurity in regard to our knowledge of idioplasmic mechanism we certainly cannot rationally speak of a "direct cause." Therefore we cannot recognize a theory of direct cause for the existence of and descent of plants in the sense that this existence is a natural result, and not a special creation. The micellar constitution of idioplasm, which gives rise to the processes of life, must be designated as a special gift of the Creator. Nägeli admits that the primordial plasm is converted into idioplasm by the *given* (inherent) molecular forces. As Nägeli states that there are causes inherent "by nature" in the idioplasm, so we likewise, from the idealistic point of view, state that this or that happens according to nature. We, however, wish to imply that the natural laws as well as matter itself are derived from God, and therefore we speak of the existence of a special creation, and not of a natural necessity, which controls all. We will even go so far in the use of language, in so far as we are dealing only with the natural laws of creation, that we will not speak of "miracle," although we believe in the miraculous creation and preservation of the universe by the Creator. We leave the pale of science only when the sum-total of scientific investigations fails us.

Although Nägeli has clearly shown the fallacies of Darwin's theory, he has allowed himself to fall into gross errors in regard to his own theory (for example, in regard to the influence of external stimuli, the behavior of idioplasm). His logical mind, however, finally led him to that substance whose mechanism we cannot understand, but which science has long considered as the sustainer of the various life-phenomena, namely, *plasm*. In this substance we also believe the forces to be concentrated which enter into the phenomena of life and growth.

With idioplasm, the structure and mechanism of which Nägeli considers the "greatest mystery in the doctrine of descent," we also associate the miracle of creation; we know that "living plasm" is necessary for the existence of a living cell, and hence for every living plant. "Mystery" and "miracle" are the two contrasting terms. Let our opponents not be misled: idealist and materialist both fail to comprehend the natural causes of certain things. The idealist knows from experience that the thorough investigation of any phenomenon in nature will sooner or later meet with conditions which must be looked upon as *given*. The materialist ignores this experience, does not explain the "mystery," but still maintains that the ultimate causes are capable of a natural explanation without miraculous intervention. Is it not well for the human mind, which is only a breath of the creative Spirit, to recognize one's Creator in nature? Is it, then, intellectual weakness to acknowledge the Almighty? Why did Nägeli write, "To deny spontaneous generation is to declare the miracle"? Although we declare the miracle, we are stricter empiricists than our opponents; we also value scientific investigations which bring to light truths which the human intellect can arrive only at after much toil.

APPENDIX.

The Life-period of Plants.

1. The *Schizomycetes* live about 3½ hours on the average, after which the individual divides (Nägeli and Schwendener).

2. *Moulds* and microscopic algæ live from several days to several months.

3. Many plants live one or two, more rarely several, "vegetative periods," which vegetative period may extend over a period of from ¼ to ¾ of a year. Winter in the temperate zones and the dry period in hot climates is the time of vegetative rest or seed-rest. Accordingly we speak of annual, biennial, or perennial plants (see p. 158).

We also find that biennial plants of our climate become annual in warmer climates; perennial plants of warmer climates sometimes become annual in our climate (*Ricinus*).

4. Tree-like plants sometimes reach an old age. Of our indigenous trees the linden, oak, pine, and yew may become 1000 years old, the yew even 3000 years. Among conifers the ages of *Taxodium distichum* (Mexico) and *Wellingtonia gigantea* (California) have been estimated at 4000 years. Of monocotyledons, *Dracæna Draco* (Teneriffe) reaches the age of several thousand years. The climax of mass development and age is reached in *Adansonia digitata* (Africa), which is said to live 6000 years. At the moderate height of 9–12 m. this tree measures 30 m. in circumference, and has branches 15–18 m. long (Seubert).

We are in doubt as to the exact age of many subterranean rhizomes and perennial plants, since we have not actually observed how long a rhizome *may* live.

PART V.

THE GENERAL CHEMISTRY AND PHYSICS OF PLANT-LIFE.

I. CHEMICAL PHYSIOLOGY.

In the treatment of tissue-physiology (II, B) we also took into consideration some very important chemical processes, such as assimilation and the formation of albuminous compounds. It now remains for us to consider the more important features of the general chemistry of plants. (In the main we will follow PFEFFER and SACHS.)

As a rule, the first step in making an analysis of a plant-substance is to place the substance to be examined in a desiccator. The determination of the dry substance and water of different plants gives widely different results, depending upon the conditions of development. Ripe seeds contain comparatively little water, the dry substance constitutes about $\frac{8}{9}$ of the entire weight. while in the germinating seed, after the reserve material has been absorbed, it is scarcely $\frac{1}{10}$; later the weight of the dry substance may again increase from $\frac{1}{8}$ to $\frac{1}{5}$. In submerged plants there is of course but a very small amount of dry substance, often less than $\frac{1}{10}$.

On burning the plant only a small percentage remains as ashes. This important statement implies that almost the entire mass of the dry substance must consist of combustible or volatile elements or compounds; the elements are C, H, N, O. S remains in chemical union with the ash, forming basic oxides, similar to the readily oxidizable P.

What are the substances appropriated by the plant, and how are they appropriated? What substances are absolutely necessary, and why?

C, H, O, N, also K, Ca, Mg, P, and S, are the elements of which the food-substances are composed. Na, Cl, and Si seem to belong to the group of useful rather than necessary elements. Among *fungi*, rubidium and cæsium may be substituted for K; Mg, Sr, or Ba for Ca. Fungi may subsist without Fe, since they contain no chlorophyll. Marine-plants contain iodine and bromine in addition to the elements mentioned above.

Among plants O and N are the only elements which occur in the free state—N as a gas, O as a gas and in solution in water. The remaining elements occur almost exclusively as binary, ternary, or even higher compounds.

Since *plasm* is chemically closely related to albuminous compounds, and since the *cell-wall* and starch consist of carbohydrates, it becomes evident that C, H, O, N, S are the *necessary* elements, eventually also P.

Oxygen alone enters into the plant-metabolism as an *element*. *Iron* enters the plant in the form of an oxide in solution. It occurs only in small quantities, though it is absolutely necessary in chlorophyll-formation and therefore also in assimilation. *Sulphur* and sometimes *phosphorus* are necessary in the formation of albuminous substances. *Potassium* and *calcium* are also necessary, though their true significance is not understood. (See below.)

According to BOUSSINGAULT, the free nitrogen of the air cannot be utilized as food by the plant. It is usually introduced into the plant by way of the roots; not in the free state, but in the form of compounds, such as nitrates, nitric acid, and ammonia in solution in water. In the years 1851–1854 Boussingault apparently demonstrated the fact that when all nitrogen-bearing compounds were excluded from the soil and atmosphere, the elementary N did not increase the nitrogenous compounds of the plant; the plant would die after all the reserve nitrogen in the form of compounds had been utilized. This belief prevailed until recent years, when VILLE, JOULIE, ATWATER, FRANK, HELLRIEGEL, and others carried on experiments which tend to prove that the free nitrogen of the air may be utilized by the plants. FRANK based his conclusions upon experiments with algæ, fungi, and several phanerogams. He has demonstrated that not only are leguminous plants which bear root-tubercles containing fungi (rhizobia) capable of assimilating free nitrogen, but also non-leguminous plants, as opposed to the conclusions of Hellriegel.

We will now return to the important nitrogen-bearing compounds. According to Boussingault, phanerogams appropriate *nitric acid* more readily than they do ammonia; for some fungi *ammonia* is better suited than nitric acid (Pasteur, A. Mayer, Nägeli).

Sulphur and *phosphorus* enter the plant in the form of sulphates and phosphates.[1]

The two binary compounds CO_2 and H_2O supply the plant with the elements C, O, and H. CO_2 is almost exclusively taken from the atmosphere, H_2O almost exclusively from the soil. The process of assimilating CO_2 and H_2O necessitates the presence of chlorophyll and the aid of sunlight. For each volume of CO_2 assimilated there is liberated an equal volume of O. The most common product of assimilation among dicotyledons is starch (amylum), which occurs in the form of small grains. If we consider $C_6H_{10}O_5$ as the formula for this compound, the reaction may be represented as follows:

$$6CO_2 + 5H_2O = C_6H_{10}O_5 + 12O.$$

In other instances (many monocotyledons) a form of sugar seems to take the place of the starch (see pp. 122 and 131).

So far we have not been able to follow the process of assimilation in its various phases. In the circulation of food-substances within the plants, the processes of catabolism, such as converting starch and cellulose into sugar, decay, etc., are much better known than the processes of metabolism (assimilation and various processes of transformation. (See p. 258).

At present we have not a clear understanding of the part that chlorophyll plays in the process of assimilation. In the discussion of the assimilating system we learned that the influence of light varied with the wave-lengths (color); this relation was made clear

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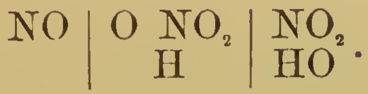
[1] According to Sachs, the following is a very satisfactory culture-fluid for plants:

Water	1000.0 cu. c.
Potassium nitrate	1.0 gram.
Chloride of sodium	.5 "
Sulphate of calcium	.5 "
Sulphate of magnesium	.5 "
Phosphate of lime (finely pulverized)	.5 "
Chloride of iron	a few drops.

by **Engelmann**'s interesting bacterial experiments, which confirmed the old theory of **Lommel**. We shall now return to the nitrogenous foods.

The following are natural sources of nitrogenous compounds.

1. The electric spark passing through dry air produces NO; this immediately unites with the O of the atmosphere and forms NO_2; the latter unites with water to form nitric acid:



$$\mathrm{NO}\;\left|\;\begin{array}{c}\mathrm{O\;NO_2}\\ \mathrm{H}\end{array}\;\right|\;\begin{array}{c}\mathrm{NO_2}\\ \mathrm{HO}\end{array}.$$

2. In various processes of combustion ammonium nitrite and ammonium nitrate are formed (NH_4NO_2, NH_4NO_3).

3. Ever since animal creation the decay of animal substances has been the source of important nitrogenous compounds, especially NH_3 (ammonia). Connected with this process of ammonia-formation is

4. The production of saltpetre (potassium nitrate), as follows: NH_3 takes up O in the presence of an alkali; that is, the oxidation of NH_3 forms a nitrate, as KNO_3, $NaNO_3$; the latter occurs very plentifully in Chili.

The formation of albuminous substances in the plant has already been discussed.

Mineral Food-substances.—The essential minerals are K, Ca, Mg, Fe (S and P were mentioned above). The agricultural importance of phosphate of lime, of the sulphates, and of the lime-salts are well known. Cl, Na, and Si are *useful*, though not necessary.

The true use of K, that is, of its compounds, is still unknown; it always seems to be concerned in the translocation of plastic materials. It is probable that Ca plays a part in the formation of cell-walls. Mg seems to be distributed much in the same manner as K. Of Fe we know definitely that it is necessary to the formation of chlorophyll. (This seems to be the reason why fungi can do without it.)

According to the recent investigations of F. W. **Schimper**, Ca serves as a *vehicle* for the mineral acids, especially phosphoric and sulphuric acid; it furthermore prevents poisoning by preventing the accumulation of acid calcium oxalate.[1]

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[1] Flora, 1890.

With the following enumeration of *chemical combinations* and mixtures of combinations only a few explanatory statements are given; further detailed information in regard to them has already been given and may be referred to by the aid of the index.

Carbohydrates, *albuminous substances*, *tannin*, *oils*, *fats*, *wax*, *amides*, *resin*, *coloring-substances*, *ferments*.

Of the *glucocides* (whose formation and importance in the plant-economy is still unknown) we may mention amygdalin, salicin, digitatin; of the bitter extracts, lupulin and aloin.

According to PFEFFER, and more especially to DE VRIES, one physiological activity of vegetable acids, that is, their salts, is that they increase the hydrostatic pressure of the living cell by producing endosmotic action.

The nitrogenous organic compounds of a basic character, namely, the *alkaloids*, must also be mentioned. They are very frequently found in the laticiferous ducts of various plants. In the milky juice of the poppy (opium-plant) are found thebaine, morphine, and other alkaloids; in the bark of the *Cinchona* trees is found the alkaloid *quinine;* strychnine is found in the seeds of *Strychnos;* atropine, daturine, hyoscyamine in the *Solonaceæ*, etc. These compounds have a poisonous effect upon the animal organism, and may therefore serve the plant as a protection against the attacks of animals.

Resins occur not only in conifers, but also in various exotic plants. Incense is a resinous product of *Boswellia Carterii*; myrrh, of *Commiphora* (*Balsamodendron*) *Myrrha* (WARMING).

According to HOPPE-SEYLER, *cholesterin*, which is widely distributed in seeds, is a secondary (catabolic) product of the albuminoids.

Leaving chlorophyll out of consideration, there are many other coloring-substances occurring in the vegetable kingdom. We will refer only to those usually associated with chlorophyll. Red, brown, brownish-yellow, and blue-green coloring-substances are met with among various algæ. Here also belong the coloring-substances of flowers and fruits, of fungi, the coloring-substances in various barks. Examples: the kino-red of *Pterocarpus Marsupium* (FLÜCKIGER) and the coloring-substances of other woods (ebony, etc.).

In connection with the characteristic process of carbon-assimilation it must be impressed upon the beginner in the study of plant-physiology that there is a true *respiration* with liberation of CO_2 and assimilation of O, besides the usual appropriation of CO_2 and liberation of O. This true respiration is, in general, necessary for the life and growth of plants. Based upon the investigations of Boussingault, Garreau, Sachs, Pasteur, Nägeli, and Pfeffer, we may formulate our present knowledge in regard to this subject as follows.

1. If we consider the chemistry of fermentation in plants (the conversion of sugar into CO_2 and alcohol, and other similar processes) as "intramolecular respiration,"[1] we may make the general statement that no plant can live without respiration.

2. Some of the energies necessary to cell-life are due to respiration.

3. Oxygen is also necessary for the existence of some fungi if they are not supplied with substances capable of undergoing fermentation. Fermentation enables them to exist without the respiration of O; without fermentation growth ceases unless oxygen is supplied.

4. Respiration continues as long as the normal conditions of life exist; it is most active in the growing plants and growing parts of plants; for example, during germination and during the development of tubers and buds. Within certain limits respiration increases with the rise of temperature. A direct influence of light upon the respiration of chlorophyll-less parts of plants has not been observed. Chlorophyll-bearing parts of plants assimilate only in the presence of sunlight, but respire in the dark as well as in the sunlight.

"*Selection.*"

We usually speak of plants as having the ability to "select" certain food-substances. The true explanation of the meaning of this term is as follows. It has been known for a long time that different plants growing in the same environment take up the same food-substances in different proportions; for example, *Nymphæa alba* and *Arundo phragmites*, both of which grow in water or in marshy soil, and which are therefore in contact with the same soluble food-substances, take up SiO_2 in widely different proportions. The former plant contains usually less than $\frac{1}{2}$ per cent of silica, the latter usually more than 71 per cent (Schultz–Fleeth). From unknown causes inherent in the *individual* these two plants require different amounts of silica in the building up of the body-substance (deposition in the cell-walls, etc.). Due to causes inherent in the processes of osmosis the nutritive cells of *Arundo* allow more SiO_2 to enter, because it is continually removed and utilized elsewhere, while in *Nymphæa* SiO_2 is not removed from the cell. As we have already learned, the *living* primordial utricle possesses the property of being impermeable to certain substances in solution (as sugar, coloring-substances, etc.). This property is due to the inherent peculiarities of the plants themselves, and not to any "selective" power.

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[1] According to Pflüger (1875), intramolecular respiration takes place in an atmosphere free from oxygen with liberation of CO_2 *due to the breaking up of compounds within the cell*; "normal" respiration is accompanied by oxygen-assimilation.

The Cyclic Course of Food-substances.

The entire chemism of plants may be diagramatically represented upon a circular line, dividing it into quadrants as follows: 1, assimilation; 2, transformation; 3, retrogressive changes; 4, decomposition. 1 and 2 are metabolic processes, 3 and 4 catabolic (Nägeli).

CO_2, H_2O, and NH_3 (or HNO_3) figure as raw material in the first process and again appear as the final products in process 4, in decay, fermentation, etc. Processes of *transformation* convert the carbohydrates and amides of process 1 into more complicated chemical compounds, as cellulose, albuminoids, fats, ethereal oils, etc. *Retrogression* (3) works in the opposite direction; cellulose is changed into sugar, fats into fatty acids and glycerine; glucocides are also split up into sugar and some other compound. The products of decomposition (4) are again the simpler compounds CO_2, H_2O, NH_3.

II. THE PHYSIOLOGY OF GROWTH.

Scientific botany, like other special sciences, finds its greatest difficulty in solving those problems which lie nearest at hand. What is growth? Why *must* cells grow? These are questions which the physics and chemistry of plants have failed to answer satisfactorily. Growth, the specific manifestation of life, like all other vegetable life-phenomena, can be traced only to *plasm*, in which it is inherent. There is no mechanics of plasm which enables us to deduce from the structure and peculiarities of plasm what actually occurs in the growing cell. This statement is to be emphasized, because efforts have not been wanting to explain the growth-phenomena in cell-life[1] from a purely physical basis. (See below.)

A cell must have a certain degree of turgor as a necessary condition of surface-growth; hence turgor is a phenomenon always accompanying surface-growth. Frequently the ratio of growth proceeds parallel with the turgor-force (DE VRIES). Our knowledge of turgor is, however, far from sufficient to give us a clear conception of growth. There are certain substances known to physiological chemistry which form vesicular deposits, the so-called membranes of precipitation, as, for example, lime solution and tannin, sulphate of copper and potassium ferro-cyanide. To these "inorganic cells" (vesicles) the "turgor-growth" theory is to a certain extent applicable: taking up of water by endosmosis causes the artificial membrane to expand and finally to rupture. At this rupture the solutions within and without at once form a new membrane of precipitation; this may be repeated again and again. A cylindrical algal cell, however, differs very materially from such artificial vesicles, because it has a cellulose-membrane and plasmic utricle, and the cell-wall can grow only with the aid of the plasm. In its chemical nature the membrane is not merely a precipitate from the albuminous substances and water. Continuing the comparison, one would expect that the cylindrical cell would become nearly spherical in a short time because of the equal expansion in all directions. Actually it elongates in one direction, which indicates that a difference in the expansion of the cell-wall in different directions is one of the conditions of cell-growth.

A. ZIMMERMANN[2] gives a brief summary of the efforts made by different authors to give a mechanical explanation of the form and position of cell-walls. We must *estimate* the work of BERTHOLD and ERRERA especially. I say "estimate," because it is very important that we should not draw other conclusions than such as really follow from the results of their investigations. According to Zimmermann, the following may be looked upon as being established by the investigations of Berthold and Errera.

It is an empirically derived rule rather than a generally established fact that the cell-wall during cell-division begins as a surface of smallest area. Although the young cell-aggregates resemble the vesicles of soap-suds in their arrangement and in the position of the walls,[1] yet it must not be assumed that this offers a mechanical explanation of cell-wall formation. The attempt to explain the mechanics of the exceptions to the rule seems especially futile. Further, every anatomist knows that in the development of plants and plant-organs we are not only concerned with cell-aggregates which are divided by surfaces of least area: the cell-walls are intimately correlated to the form of the organs as well as to the ultimate function of the cells. All that we can comprehend of this correlation is that it serves a specific purpose. Berthold himself does not give an exact mechanical explanation of the arrangement of cell-walls.

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[1] BERTHOLD, Studien über Protoplasmamechanik, Leipzig, 1886.—TRANS.

[2] Beiträge zur Morphologie und Physiologie der Pflanzenzelle, Tübingen, 1891, Heft 2.

The growing cell-wall (for example, of *Spirogyra*) can not be compared to a liquid layer, as ERRERA has done; the only resemblance is that of form. ZIMMERMANN summarizes NÄGELI and SCHWENDENER'S (Microskop) explanations of the causes of the cell-forms. According to these authors each cell and each cell-complex has a tendency to assume a spherical form due to hydrostatic pressure. Although this is in harmony with the view that the cell-walls form surfaces of smallest area, yet the authors did not believe that they had discovered a fundamental principle of the mechanics of plasm. If we consider how various the growth-processes of a cell are, we will refrain from expressing the opinion that the majority of growth-phenomena can be explained mechanically. In one case the cell grows in length, in another it expands into an oogonium; again, it branches; here it may grow and not divide; it may divide and not grow; again, it may grow in thickness only, either locally or uniformly; etc. We have not a thorough understanding of a single phenomenon of growth.[2]

Although there is no satisfactory explanation of growth, and no mechanics of plasm, there is a *physiology* of growth. We shall briefly mention the more important facts in regard to it.

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[1] PLATEAU'S "Gleichgewichtsfiguren."

[2] SCHWENDENER made the following important statements: "He who endeavors to solve some definite problem and who in the course of his investigations meets with insurmountable difficulties has at least found a valuable insight into his work, and his fellow-workers will be much indebted to him if he makes known his experience. But he who does not see the existing difficulties and who believes he has found the *final* explanation when in reality only misunderstood processes are described, tends to confuse the mechanical-physical investigation rather than to promote it." (Rectoratsrede, Berlin, 1887.)

Phenomena of *growth* and *movement* in the vegetable kingdom are difficult to separate. Naturally there is movement with every process of growth, though every movement is not accompanied by growth.

A. ACTIVE AND PASSIVE GROWTH.

There is an active as well as a passive growth. The cambium-ring of trees and the young portions of roots show the best examples of active growth. The energy exerted by the growth-processes of the cambium has not been definitely determined. From KRABBE's investigations[1] it would seem to be considerable in trees with deciduous leaves; the growth-pressure at certain periods rises to fifteen atmospheres.

The cortex also shows phenomena of *passive* growth induced by the tangential tension proceeding from the cambium (KÖPPEN),[2] besides the active growth observed in the cork-cambium. A visible result of this tangential tension is the broadening of the medullary rays in the cortex; from this we may conclude that mechanical tension can be converted into growth. It is easy of demonstration that an originally straight stem may become permanently crooked by processes of passive growth when the growing portion of the stem is retained in a crooked position. Similar processes occur in the winding of climbing plants and tendrils. Such permanent curvatures are, however, induced by special energies which will be discussed later.

B. THE RESULTS OF UNEQUAL GROWTH.

According to DE VRIES (C. SCHIMPER), the term *epinasty* refers to a relatively stronger growth of the upper side of an organ, *hyponasty* to a stronger growth of the lower side. If these inequalities occur in an organ growing in length, curvatures will appear; when they occur in organs growing in thickness, as, for example, in horizontal branches of trees, there is produced a woody body with *eccentric* pith.

Unequal growth of different tissues in one and the same organ produces a series of phenomena which will now be briefly discussed.

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[1] Abhandl. der Berl. Akademie, 1884.

[2] Nova Acta d. Ksrl. Leop.—Akad , LIII.

Tissue-tension may be mentioned as the *first* result of unequal growth.

(*a*) *Tissue-tension.*

To illustrate this phenomenon a longitudinal section may be cut from the middle portion of a growing stem or petiole (*L* in Fig. 170, *a*). A vertical surface view of this section is shown in *b* and *c*. The medulla *m* and cortex *r* do not cease to grow at the same time as the woody tissue *h*. In the uninjured organ this difference must produce tensions; the woody elements are passively elongated and continually strive to contract; the cortical and medullary cells are hindered in their growth, are compressed, and continually strive to elongate.

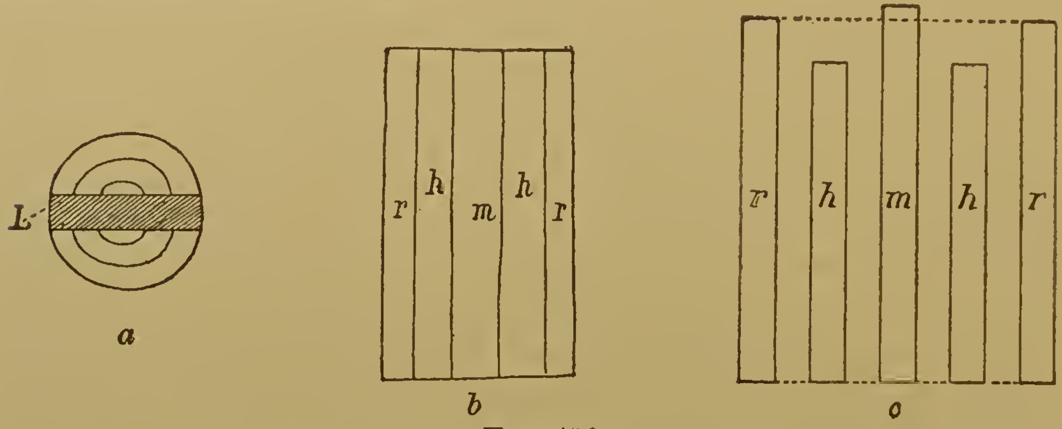

FIG. 170.

Isolating the individual parts of the section verifies the above statement by the shortening or elongating of the various elements. For the same reason the bisected organ curves outward. The medulla elongates more than the cortex (*c*). Increasing the turgor by placing the section in water will further increase the curvature. Corresponding phenomena may be observed in transverse sections.

From what has just been stated it follows that tissue-tensions are produced by a decrease and increase in the turgor[1] as well as by unequal growth. The following remarks will have a bearing upon tissue-tension due to turgor. The form of the cells and their expansibility in different directions influences the phenomenon of tension in a high degree. In those roots which become shortened in the turgescent state and elongated in the wilted state, we must assume that the cell-walls are more expansible in the transverse direction; that is, the individual cells of the root-parenchyma become shortened and much expanded laterally. The root-cortex remains passive during this process of shortening and becomes transversely wrinkled. The purpose of such shortening of roots is quite evident. For example, a rosette of radical leaves (cataphyllary) which, according to their structure and for mechanical reasons, should remain near the ground will thereby remain in the same position, although a short portion of the stem below the leaves elongates somewhat. Such shortening also tends to hold the plants more firmly in the soil. This phenomenon received a special significance from the observations made by FITTMANN (1819). The winter-buds of biennial plants whose cotyledons and plumules are already above the soil may withdraw them into the soil on the approach of winter. H. DE VRIES has explained the mechanics of this phenomenon.

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[1] According to N. J. C. MÜLLER, a hydrostatic pressure of 13½ atmospheres can be demonstrated in the medullary cells of *Helianthus;* according to AMBRONN, 9–12 atmospheres in petioles of *Fœniculum.*

As a second result of unequal growth within an organ we may mention

(*b*) *Curvatures.*

Curvatures of cylindrical or prismatic organs[1] take place when any given longitudinal portion of tissue elongates or shortens more than does a similar portion on the opposite side. It is evident that all such curvatures are not dependent upon processes of growth, since shortening may also be due to evaporation of water, and elongation may be due to an increase in the amount of water taken up. Such curvatures do not come under the category of "unequal growth." Curvatures due to unequal growth are, however, of very frequent occurrence.

Leaving out of consideration the frequently occurring foldings of cell-walls, as, for example, the "wavy" epidermis, the anatropous seed-buds, etc., we shall refer more particularly to those curvatures caused by *one-sided exposure to light* (heliotropism), by the *one-sided action of gravity* (geotropism), or moisture (hydrotropism). These are conditions which influence the growth of plants in a high degree. The significance of the curvatures mentioned above is very evident when we study the normal assimilating organs, the roots, etc. The leaves must assume a position most favorable to the influence of sunlight; roots and other subterranean organs must be conducted into the soil. The "nyctitropic" curvatures also belong here.

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[1] See NAGELI and SCHWENDENER's Mikroskop.

To decide whether a given curvature or phenomenon of growth is due to the influence of sunlight or gravity we must resort to physiological methods of investigation. The clinostat is the best instrument to aid us in deciding the question. This apparatus consists of a clockwork in which a flower-pot with a plant takes the place of the hand on the dial. It is at once evident that an hourly rotation upon a vertical axis continued for days will eliminate the influence of one-sided illumination; also that a long-continued rotation on a horizontal axis will eliminate the influence of gravity. All that is required is to change the position of the plant frequently enough, so as not to allow any perceptible growth which might result from the causes referred to.

(*c*) *Torsion.*

A third, and the most complicated, result of unequal growth within an organ is torsion.

An organ is said to be twisted (tordiert) (Nägeli and Schwendener,[1] Schwendener and Krabbe[2]) when the originally longitudinal lateral lines assume a spiral course. There are two kinds of torsion, real and apparent. An *apparent* torsion may be caused by curvatures in the successive planes of an organ; here, also, the originally longitudinal line takes a spiral course, but there is no transverse displacement of the cells, such as always occurs in true torsion. There is a form of false "torsion" noticeable in some tree-trunks in which the woody fibres take a slanting position, caused by the cambial cells growing past each other. The general direction of the trunk or branch is thereby not changed. In *true* torsion the successive transverse disks glide upon each other. Both forms of torsion are of frequent occurrence in the vegetable kingdom, and it is often very difficult to determine quantitatively what is true and what is only apparent torsion.

The following causes may produce true torsion: (1) the more rapid elongation of outer tissue-layers or the shortening of inner tissue-layers; (2) elongation of the cells in a direction diagonal to the longitudinal axis of the organ; (3) the cells of the entire organ may tend to twist. All are the result of processes of growth.

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[1] Microskop.

[2] Über Orientirungstorsionen.

According to Krabbe and Schwendener, the second and third causes producing torsions are active in those adaptive torsions which bring dorsiventral leaves in a favorable position with regard to light, and which cause zygomorphic flowers to assume a suitable position for being visited by insects. The living plasm may be so influenced by gravity or by light[1] that the growth of the cell-wall of the individual cell may increase or decrease in a direction diagonal to the longitudinal axis. This gives the individual cells a tendency to become twisted. According to these authors, there is therefore besides heliotropism a *heliotortism*, besides geotropism a *geotortism*. Under normal conditions gravity alone is active in causing plant-organs to assume a definite position with regard to its supporting axis or the radius of the earth; but in order that plant-structures may assume favorable positions in regard to light, light and gravity must act together, at least in a number of instances, while in other instances light alone is capable of bringing about the necessary torsion. I will add a few more statements from the important work of SCHWENDENER and KRABBE to show how readily superficial considerations seem to make it possible to explain from a physical or mechanical basis the most important phenomena of plant-life.

1. An immediate causal relation between the adaptive movements of leaves and flowers on the one hand and light and gravity on the other does not exist; rather the cause and effect are linked together by the *unknown irritability* of plasm.

2. The authors mentioned differ from DE VRIES in the explanation of the phenomenon due to the amputation of leaves. Among many of the plants with crossed opposite leaf-pairs (*Philadelphus*) the leaf-blades on the horizontal branches are brought into the required light-position by a torsion of the internode; in addition the leaves must also become twisted upon the petiolar axis to bring the leaf-blade into the proper position. The active factor in bringing about these movements is the sunlight. If the lower leaf of the normal internode (not twisted) is removed, torsion will proceed as usual; but if the upper leaf is removed no torsion takes place in

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[1] According to Schwendener and Krabbe, there are torsions due to the combined influence of light and gravity. The manner in which these two forces act is little understood. (Compare the subsequent statements in the text.)

the internode or in the remaining leaf, for *such torsion would be without a purpose.* Further, the internode following does not become twisted, as might be expected, because the new leaves are already in the proper lateral position. The weight of the remaining lower leaf does not suffice to explain this phenomenon, since the growth-processes due to gravity would suffice to overcome the weight of the remaining leaf.

3. The following is another interesting result obtained by Schwendener and Krabbe. *Theoretically* a leaf or flower needs, at most, to turn upon its axis 180° in order to bring it in a favorable position for light, etc. Careful observations have, however, shown that long stems may turn from 500° to 700°, while the organs concerned retain their chosen adaptive position. If, after having acquired the necessary amount of torsion, the organ becomes further twisted by processes of growth, it is found that the excessive torsion is again undone in the upper part of the petiole or peduncle. This is another interesting example showing that adaptability may be revealed by physical-physiological investigations, and that the teleological law is not seriously shaken, as often happens to the "biogenetic law" (HAECKEL).

C. MOLECULAR ORGANIZATION OF PLANT-STRUCTURES.

(APPENDIX TO THE CHAPTER ON THE PHYSIOLOGY OF GROWTH.)

The following German botanists have made a special study of this difficult subject: MOHL, N. J. C. MÜLLER, WIESNER, DIPPEL, VON HÖHNEL, ZIMMERMANN, AMBRONN, and especially NÄGELI and SCHWENDENER; among specialists in other fields, V. EBNER.

Some of the problems relating to this subject were touched upon in the discussion of growth by intussusception (starch-grains and cell-walls). The following statements are based upon the results of the investigations of the authors mentioned.

1. According to Nägeli's micellar theory all bodies capable of swelling (in botany we mean especially the starch-grains and cell-walls) consist of *micellæ* or aggregates of micellæ.[1] During

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[1] According to Nägeli, chemical molecules unite to form molecular masses of higher order. If this molecular union takes place after a definite method (as, for example, the union of a salt with water of crystallization) the resulting molecular

imbibition each micella surrounds itself with a layer of water of a given thickness; in complete desiccation the micellæ lie in contact; in general their form is polyhedral. If water enters between the micellæ it indicates that the attraction or cohesion between water-molecule and micella must be greater than the attraction of the micellæ for each other; according to Nägeli the attraction between water-molecules and micellæ decreases more rapidly with the distance than does the mutual attraction of the micellæ; after a time the latter will predominate: this is the point of maximum imbibition. (REINKE'S experiments show what enormous forces are exerted by the processes of imbibition in such organized bodies. Swelling of the cell-walls of *Laminaria* indicated a pressure of forty atmospheres.)

2. Every normal cell-membrane which has passed its earlier stages of development is, as a rule, *doubly refractive.* According to BRÜCKE, NÄGELI, SCHWENDENER, and AMBRONN, the cause of this is to be found in the arrangement of the crystalline, anisotropic, smallest particles, the *micellæ.* The membranes of typical mechanical cells with normal extensibility undergo no change in their optical behavior due to pressure or extension. Membranes of great extensibility when they are subject to tension show an increase in the interference of light-rays. It may be probable that in the latter case the optical difference is due to a reticular arrangement of the micellæ (SCHWENDENER). If such is the case it is in favor of the theory of "anisotropic micellæ" (MEYER, 1895).

V. EBNER and others, and in partial agreement with them, ZIMMERMANN, suppose the cause of this double refraction of some cell-membranes, to lie in the systematic arrangement of isotropic micellæ, without, however, being able to give any definite explanation for such systematic arrangement. The evidence in support of this supposition is based upon the observation made on the above-mentioned highly extensible cells, without including any substances not pertaining to our subject, as bones, cartilage, etc.

In reference to the "molecular tensions" which VON HÖHNEL assumes to exist and which are supposed to cause the phe-

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mass is called a *pleon* ("Pleone"). The micellæ are either simple aggregates of molecules or *pleon-aggregates.*

nomena of double refraction, I will add the critical observation of Schwendener. The existence of unequal or one-sided molecular tensions in the smallest particles of the membrane (the micellæ) cannot be assumed, because we cannot conceive of them as having points of fixation.

3. The arrangement of the axes of the optically active ellipsoids of elasticity of the cell-membrane always coincides with morphologically definable directions: one axis is always radial; the other two lie in the tangential plane, of course extending in different direction. The radial axis is usually the shortest.

4. The shortest optical axis of elasticity always coincides with the axis of maximum swelling; least swelling is in the direction of the optical axis of greatest elasticity. If the micellæ are of unequal dimensions in the different directions and are all surrounded by equally thick layers of water, it will be readily seen that the expansion must be less parallel to the longest axis of the micellæ than to the shortest axis.

III. TEMPERATURE, LIGHT, GRAVITY, AND OTHER FACTORS, IN THEIR RELATION TO PLANT-LIFE.

A. Effects of Temperature.

The discussion of the effects of temperature and light will in general be based upon the results of the investigations of Nägeli, Sachs, Pfeffer, and Frank.

(*a*) *Production of Warmth and Cold.*

Processes productive of heat and cold occur within the plant. As a result, plants give evidence of a subjective temperature; that is, under certain conditions their temperature is different from that of the surrounding medium. Respiration, that is, the conversion of hydrogen- and carbon-bearing compounds into CO_2 and H_2O, produces a rise in temperature. In an extreme case (flowers of *Aroideæ*) the rise in temperature may be 15° C. During the germination of barley the temperature also rises, as is well known. Evaporation of moisture from the plant tends to reduce the temperature.

(*b*) *The Effect of Temperature upon Plant-life.*

As every chemical process takes place in a certain temperature, so likewise are the various life-processes of plants dependent upon certain temperatures; among different plants the same life-process may be dependent upon different temperatures. However, the temperature suitable to a given process may vary considerably, so that we usually speak of a minimum, *optimum*, and maximum temperature. According to SACHS, these three "cardinal points" for the germination of our cereals are approximately at 0°, 28° (optimum), and 40° C.

In reference to experimental physiology it may be mentioned that there are special apparatus for the determination of the rate of growth within definite periods of time. Such are the auxanometers of SACHS, WIESNER, and BARANETZKY.

Below the optimum the curve of growth rises and falls with the temperature-curve. The curves at least tend in the same general direction, though they may not be parallel. It, however, requires great care to determine the influence that each individual factor has upon growth. Some observations in regard to these difficulties will be in order. When observing the influence of a constant temperature upon the growth of a plant which is at the same time exposed to a variable illumination, for example growth during day and night, we encounter a complication (SACHS[1]). The shoot-axis of *Dahlia*, for instance, shows a maximum growth in the early morning; in the afternoon a reduction; before sunset another increase. It is evident that in this case the growth-curve would not extend parallel with the temperature-curve. According to the observations made by SACHS and BARANETZKY, there is a periodicity of growth independent of temperature and light, which is manifest in a rise and fall extending over a variable period of time. The most important and most general phenomenon in this periodicity due to internal causes is the *grand period of growth* (Sachs): each transverse zone of a root, of a stem, etc., begins to grow slowly, then grows more rapidly, and after having reached the maximum gradually decreases until it ceases to grow entirely. Such periodicity is not due to external causes.

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[1] Vorlesungen, p. 680.

Effects of Extreme Temperatures.—Seeds of plants in a dry state, may withstand very low temperatures. The same is true of spores, yeast-cells, and the *Schizomycetes.* Well-dried seeds may resist a temperature of 120° C. without losing the power of germination. "Sterilization" in bacteriology requires that liquids should be boiled for hours in order to kill all the germs of fungi, or exposed to dry heat at 130° to 140° C. for a longer period.

In general it may be stated that plants and parts of plants with a low percentage of water will withstand the extremes of temperature better than succulent plants. Lichens, for example, will resist the extremest cold of winter. Winter wheat, without being covered by snow, will resist a temperature of −10° C., or even lower ; *Coleus* is killed by a temperature of 1° to 1.5° C. Succulent plant-portions of various phanerogams are killed by a temperature of 45° to 50° C.

Freezing does not always kill the plant ; death sometimes results during the process of thawing. If this process is allowed to proceed slowly the life of the plant may continue. Freezing inhibits turgescence, that is the water within the cells escapes into the intercellular spaces. As a rule, ice-formation begins outside of the cells, in the intercellular spaces, when the temperature sinks slowly to −5° C., or even lower. A sudden and excessive fall in the temperature causes rupturing of the cells and tissues, due to the pressure of the rapidly forming ice-crystals. When the process of thawing is sufficiently slow the water is again taken up by the remaining living cells. However, according to FRANK and MÜLLER-THURGAU, death may result during the process of freezing.

B. EFFECT OF LIGHT.

(*a*) *Production of Light.*

Many plants and parts of plants are luminous in the dark ; for example, certain fungi (bacteria). Since this phenomenon ceases on the exclusion of O, it is in all probability a process of oxidation.

(*b*) *Influence of Light upon Plant-life.*

The difficult problem which we will encounter in this chapter, as well as in the corresponding chapter on gravity, is that the same causes do not produce the same effects in all living cells, but rather produce effects which, to external appearance at least, are directly opposite. The evidence that the principle of adaptation is the controlling factor in such phenomena is so conclusive, that the investigations which stand at the very height of purely scientific and causal-mechanical methods lead to the same conclusion.

Here also we must speak of a minimum, optimum, and maximum effect of light upon the various organs and life-processes. Elementary physics teaches us that we not only have to deal with the effect of various *light-intensities*, but also with the effects of different *wave-lengths* (hence colors).

In general, chlorophyll-formation requires less light than chlorophyll-activity (assimilation): the former process, the turning-green of plants, may even take place in the dark; for example, in ferns and in the seedlings of conifers. Coloring-substances of flowers may also be formed in the dark, provided the necessary assimilated substances are present, or their formation made possible (SENEBIER, DE CANDOLLE, SACHS). Sachs further found that the floral buds of *Tropæolum* require the ultra-violet rays for their development. With the aid of these rays the flower-forming substances would be produced in the green leaves (Sachs). The relation of wave-length to the function of assimilation has already been explained (Part II, B). The highest optimum (there are two maxima of assimilation), according to ENGELMANN, lies in the red spectrum. The rays passing through ammoniacal oxide of copper, hence the highly refrangible rays, are most active in the phenomena of growth and plant movement (movement of chlorophyll, heliotropism). They resemble more nearly the activity of normal daylight.

Effects of Abnormal Illumination and the Conclusions derived therefrom.—Plants which are normally subject to the change of day and night on exposure to continuous darkness show a variety of effects upon the different organs. The pathological phenomena usually depend upon deficient nutritive changes.

Let us consider the behavior of the potato-plant, according to the observations of Sachs.[1] The young shoots (the "eyes") of the tuber require darkness for their growth; light hinders their development in a remarkable degree; later the different members and leaf-organs developing from them must have sunlight for their normal development. The shoots first named are adapted to grow in darkness; from them the tubers are developed. Many other subterranean organs do not show this sensibility to light. Let us consider two simple experiments. 1. Observe the growth of seedlings and shoots in permanent darkness. 2. Place one part of a plant in the dark, while the remaining parts are normally illumined (according to the experiment by SACHS). In these cases growth in the dark can take place only at the expense of the reserve-materials or of food-substances formed in adjacent tissues under normal surroundings. In case the seedlings and shoots show a rapid growth of the axial organs they become abnormally elongated, with usually slight development of the mechanical cells. The leaves remain dwarfed, but this is not directly due to the lack of sunlight, for case 2 shows that leaves may develop on the darkened plant portion, though they may not be of normal size. The darkened portion (2) may even develop normally colored flowers and fruit. In both cases and in general it may be stated, that leaves developed in the dark are *devoid of chlorophyll;* they are said to be "chlorotic," or *etiolated.*[2]

From the study of these pathological changes and the peculiar differences associated therewith we are enabled to understand their teleological significance. Cotyledons which normally remain under ground, and therefore do not become very much elongated in the hypocotyledonous stem-portion, do not show any abnormal elongation in permanent darkness. On the other hand seedlings whose cotyledons are normally raised above the soil show the described elongation when growing in the dark. Again, not all foliage-leaves remain small in the dark; many blade-like monocotyledonous leaves become abnormally long and slender in the dark. This is also true of the leaves of the onion; by their elongation they are enabled to rise above the ground from their low position, and may push their way out of the leaf-sheaths.

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[1] Vorlesungen, p. 650.

[2] SACHS, Abhandlungen über Pflanzen-Phys. p. 194. (1892.)

The following phenomena come under the same teleological category. 1. Many plants show little or scarcely any growth in the dark. 2. Roots, in general, grow more rapidly in the dark than in the light. 3. Many fungi can grow only in the dark. Of the latter we know that light is not a factor in their nutrition. In the case of roots we know from observation that their *normal* growth takes place in the dark. In regard to 1, many cases are yet not satisfactorily explained; but it is very clear from physiological evidence that many fern-spores require light for their germination (BORODIN and others); this is also true of the spores of some mosses (BORODIN, LEITGEB). In these cases the products of germination can only continue their growth with the aid of sunlight.

Phototonus is the term applied to the normal reaction of plants to the rhythmic change of light and dark (day and night). A longer or shorter exposure to dark will temporarily destroy this phototonic condition, producing a transitory state of rigidity (Dunkelstarre, SACHS).

In general it may be stated that *the phototonic plants, hence normal plants, exposed to the daily change of light grow more rapidly during the dark period (night), while uniform illumination (day) retards the growth.* Special cases with explanations have already been cited.

Intimately associated with phototonus, that is, the condition produced by alternating light stimuli, is the phenomenon of "sleeping" and "waking" (opening and closing) of leaves; in other words, the nyctitropic movements. According to CHARLES DARWIN, the purpose of this movement is to reduce the radiation of heat during cold nights. Among flowers it is usually a process of closing, and also serves the function of protecting the internal organs. These movements are not always curvatures, but sometimes also torsions. We will here consider only the simple curvatures.

The mechanics of this movement, of which the following are the essential features, is only in part explained. *Growth processes* of the joints or *motile organs*, or of the nyctitropic organs without motile organs, are not the only conditions producing this phenomenon; *turgor-changes* are the essential factors. In the motile organ of the *Oxalis*-leaf there is an upper and a lower cushion of cells with an intermediate elastic vascular tissue-bundle. In the *dark* the turgor and volume of the *entire* organ increases;[1] in the light it decreases. Although the decrease and increase in the volume of the two cushions of cells begins at the same time, it *does not proceed equally fast*, so that in the dark the swelling of the upper cushion proceeds more rapidly, causing the leaf to turn downward. On exposure to light the turgor-difference is again manifest, but in the inverse order; that is, the upper cushion loses its turgidity more rapidly, causing the leaf to be turned upward by the more turgid lower cushion. The explanation of this phenomenon becomes still more difficult and complicated by the so-called "after effects." A nyctitropic plant previously exposed to the changes of day and night, when placed for days in either continuous dark or continuous light, still continues to produce to-and-fro movements. These movements, which are as yet unexplained, unite with the movements due to the change of illumination (BRÜCKE, PFEFFER, MILLARDET, SACHS).

The common garden bean furnishes a good example of this phenomenon. It need hardly be mentioned that we cannot see the causal relation between the variations in turgor and the variations in illumination. We can only establish the fact of the existence of such relative variations.

One-sided illumination acts in such a manner upon the longitudinal growth of an organ that the side exposed to the light is retarded in its growth, thus producing a curvature toward the light. Most shoots and leaves show such *positive heliotropism.* One-sided illumination may also have the opposite effect; that is, the side turned toward the light increases in growth and the organ is turned away from the light. This phenomenon, which is called *negative heliotropism*, occurs in the climbing shoots of ivy, in many aerial roots, and in some subterranean roots.

To give a causal-mechanical explanation of this phenomenon is also impossible. We feel certain that it is due to the behavior of the living cell-plasm; the question of the cause of such behavior is quite another thing. Many investigators will of course be imbued with the idea that a teleological principle also controls these relations, since this principle forms, so to speak, the keystone of our knowledge already gained and that for which we are striving. A similar difficulty in finding a causal explanation is met with in negative and positive geotropism, which we shall now discuss.

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[1] In this case the expression "sleep" does not mean relaxation.

C. Influence of Gravity.

The plant kingdom is subject to the continuous influence of gravity. Light and temperature have their variations in the change of day and night and in the seasons of the year. Gravity is a constant factor and has a great influence on plant-life.

If a growing primary root is placed horizontally, it will at once begin to curve downward at the growing part, due to the more active growth of the upper side. A portion of the stem (growing shoot) or the base of the leaf-sheath of a grass-internode[1] placed horizontally will curve upward because of the more rapid growth of the lower side. This is the so-called *positive* and *negative geotropism.*

It can readily be shown that it is gravity which causes the downward growth of roots (positive geotropism) and the upward growth of stems (negative geotropism). If the centrifugal machine is employed to counteract the earth's gravity, it is found that the root grows outward and the stem grows in the opposite direction toward the centre of rotation.

Secondary roots, branches, and leaves are controlled by other factors, since they grow in a diagonal or horizontal direction under the influence of gravity. According to Sachs, the latter organs are said to be *plagiotropic*, in distinction to the *orthotropic* stem and primary root.[2] Sachs emphasizes the fact that dorsiventral organs are plagiotropic; this one would expect when considered from the standpoint of advantageous adaptability. The horizontal position is certainly more suitable for organs with one side adapted to light and the other to comparative darkness. According to the same author, all orthotropic organs have a radial structure (see p. 166) which corresponds to the function of an equally illumined stem as well as to that of the root, which serves to fasten the plant to the soil and to take up soluble food-substances from all sides by means of the numerous secondary roots and rootlets.

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[1] Concerning this behavior of leaf-sheaths and nodes of *Gramineæ* see Part II, B, Function V.

[2] Sachs also applies these terms to a similar behavior of plants in response to light-effects.

D. ELECTRICITY. MOISTURE. WATER-CURRENTS. RADIATING HEAT.

Electrical Currents Produced by Plants.—Electrical currents have been demonstrated in the plant-body; also variation in these currents. Movements of water-currents in the plant are supposed to be the cause of the variations in the electrical currents (RANKE, VELTEN, MUNK, KUNKEL). The significance of these currents is unknown.

The following are some of the effects of the *electrical currents upon the processes of plant-life*, though no important significance has yet been ascribed to this knowledge. Electrical discharges cause cessation of the movements of the swarm-spores of *Vaucheria* (UNGER); they cause cessation of the motion of the granules in streaming protoplasm (KÜHNE, NAGELI, and SCHWENDENER); they also cause closing of the stoma (N. J. C. MÜLLER), perhaps due to changes in turgor. Strong currents may kill the cells. At this point it is well to mention BRUNCHHORST'S *galvanotropism.* Roots growing in water incline toward the negative electrode with weaker currents. Stronger currents cause the roots to incline toward the positive pole, *due to pathological influences* (ELVFING).

The observation made by SACHS that growing root-tips will turn toward a moist body (*positive hydrotropism*) is of physiological importance. The same author observed *negative* hydrotropism in stems of seedlings and in the spore-bearing hyphæ of the *Phycomyces.*

Growing roots of *Zea Mays* turn toward the current of running water (JÖNSSON, *rheotropism*). According to WORTMANN, some growing plant-portions turn toward a source of warmth (*positive thermotropism*), while others turn away (*negative thermotropism*): examples for both are found among young stems of various plants. In one and the same root a temperature below 27.5 ° C. produced positive thermotropism; a higher temperature produced negative thermotropism.

IV. THE PHYSIOLOGY OF PLANT-MOVEMENTS.

A. Classification of Movements according to Cause. The Outward Manifestation of Some Movements.

The consideration of the outward manifestation of movements in plants does not aid us in forming a rational classification of the same. The following will explain.

In general, *nutation* implies the *curvature* of an organ. To bring this about it is necessary that one side should always be relatively longer or shorter than the opposite side. Elongation of tissues (cells) may be due to growth or to the taking up of water without growth. Shortening is usually due to changes in the amount of water present, but may also be due to other causes. If the line of maximum expansion changes from side to side (with or without growth), it will cause the organ to move back and forth like a pendulum. The leaflets of *Hedysarum gyrans* describe elliptical curves (without growth).

When the longitudinal axis of maximum growth or maximum expansion remains neither on one side nor alternates from one side to the other, but *rotates* or *winds about in the organ*, it produces what is known as *circum*nutation. The organ is thereby carried around in a circle; the growing tip describes a spiral line.

Torsions also belong to the important phenomena of movement. They may also be the result of a variety of causes. The *locomotor* movements are characteristic because of their external peculiarity: entire plants or parts of plants may move about. The movements of entire plants may be explained mechanically when cilia can be demonstrated, as in various swarm-spores and bacteria; if cilia are wanting, as in *Diatomaceæ*, *Myxomycetes*, etc., it is difficult or impossible to explain the motion. As motion of parts of plants the *movement of chlorophyll* and *plasmic motion* may be mentioned as an example. The former we can comprehend at least from a *teleological* point of view. (See Function VI in the Physiology of Tissues, Part II, B.) The *causa efficiens* as well as the *causa finalis* of plasmic movement is unknown.[1] Cells of the *Characeæ* show the streaming movement of plasm very beautifully.

With these general remarks on some of the more important movements met with in the vegetable kingdom we may group them, according to cause, as follows.

1. *Locomotor movements* due to causes inherent within the protoplasm. It were better to say that the cause or causes are unknown.

2. Purely mechanical movements due to variations in the turgor of living cells or to absorption or loss of water by dead cell-walls. We will name them collectively "hygroscopic" movements.

3. Autonomous or spontaneous movements, often producing extensive changes in form and position, are also due to internal causes, such as processes of growth.

4. Irritable movements (induced movements).

We will briefly discuss movements 2, 3, and 4.

B. HYGROSCOPIC MOVEMENTS.

The term hygroscopic applies to the unequal gain and loss of water by dead as well as by living cells. Under the category of hygroscopic movements belong the opening of sporangia and anthers as well as fruits for the purpose of ejecting the seeds, spores, etc. A number of these cases have been elucidated by the investigations of SCHINZ, SCHRODT, ZIMMERMANN, STEINBRINCK, EICHHOLZ, ZOPF, and others. Since these movements have already been more or less explained in the chapters on reproduction, I will here limit myself to the following statement. Hygroscopic movements are usually due to the difference in the power of imbibition possessed by the various tissues and tissue-layers. Visible structural differences often indicate the difference in the power of imbibition. The *dynamical* cells evidently come into play here (ZIMMERMANN). These cells have a moderately thick wall, with approximately horizontal rows of micellæ which are capable of shortening considerably on drying, much more so than cells with micellæ placed longitudinally. Such cells we have learned to know as the specific (dynamostatic) mechanical cells. Should these different cells occur on opposite sides of an organ it will evidently result in bringing about a curvature. The umbels of various *Umbelliferæ* (*Daucus*, etc.) show these different cell-structures and the resulting behavior very clearly (O. KLEIN).

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[1] Attempts have been made by various investigators to explain the phenomena of protoplasmic movement, but so far not very successfully. *Chemism* and *surface-tension* of liquids are perhaps factors in such movement. See BERTHOLD'S Protoplasmamechanik.—TRANS.

As already indicated, there are cases in which the turgor of living cells causes the expansion of tissue-layers, as, for example, in the seed-coats of *Impatiens*.

To the category of purely mechanical or hygroscopic movements belong many teleological phenomena having no bearing on reproduction, as, for example, the rolling-in or folding of leaves to guard against excessive evaporation, frequently noticeable in plants of the desert (TSCHIRCH, VOLKENS, and others). In these cases the mechanical action producing the required movement is also due to changes in the turgor of living cells or to changes in the power of imbibition of the cell-membranes. Here belong the *movement of the guard-cells* of the breathing-pores, evidently due to changes in turgor (see the mechanics and anatomy of stomata). Finally, it should be remembered that the purely mechanical movements may induce either simple curvatures or torsions. (The penetration of the seed of *Erodium gruinum* into the soil is due to a process of torsion.)

C. AUTONOMOUS MOVEMENTS.

These are due to internal causes and may recur periodically, or they may occur only once or a few times during the life of the plant (PFEFFER). To the autonomous movements which occur only once or a few times belong the hook-like curvatures of growing organs, the curvatures of anthers, and the unfolding of floral envelopes. The above-mentioned circumnutation does not belong here, since this movement ceases when the plant is placed upon the clinostat (BARANETZKY). PFEFFER,[1] however, considers it an autonomous movement. According to this author, autonomous nutations are perhaps more or less present in all organs. Here we must also include the movements of the lateral leaflets of *Hedysarum gyrans* as well as the movement known as "rectipetality," discovered by VÖCHTING. This latter movement manifests itself in an effort of geotropically curved shoots to become straightened when gravity is counteracted by means of the clinostat.

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[1] Pflanzenphysiologie, p. 184.

External causes, such as temperature and light, modify the various autonomous movements.[1]

D. IRRITABLE MOVEMENTS.

What has been said in regard to the effects of gravity, light, temperature, etc., is to be applied herein so far as movements are concerned. All of the external influences of the plant-organism are *stimuli* in the wider sense; hence the heliotropic, geotropic, and also the nyctitropic movements are irritable movements in the *wider sense.* We usually recognize irritable movements in a *narrower sense*, caused by mechanical shock, or contact, accompanied by growth or without growth.

As an example of irritable movement without growth we will discuss *Mimosa pudica;* as an example of irritable movement with growth we will discuss the behavior of tendrils.

Mimosa.

Our insight into the principles of the *mechanics* of irritable and related movements due to stimuli ceases where all deep and far-reaching investigations of life-processes cease, namely, with the question, Why does the *plasm* of living cells become changed in response to certain stimuli? The *result* of this plasmic behavior—in this special case the sudden passage of water from the cell-lumen through the primordial utricle into the intercellular spaces and to the exterior—may then be considered and explained mechanically. We owe our more exact knowledge in regard to these conditions and relations to BRÜCKE and PFEFFER. The mechanical principles underlying the movements in *Mimosa* also apply to the movements in the stamens of *Cynareæ.* In

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[1] Incidentally it may be noted that there is no such contraction and relaxation in the vegetable tissues as is seen in the muscles of animals. Active shortenings or contractions are, however, not wanting; as has been mentioned, increase in turgor will cause root parenchyma cells to become shortened.

Mimosa we are concerned with curvatures of the leaf-joint (motile organ), in the stamens of *Cynareæ* with shortening of the organs. In both cases there is a sudden reduction in turgor; the primordial utricle suddenly becomes very permeable to water, allowing the water to pass through its interstices and finally also through the cell-wall into the intercellular spaces. Later this water is taken up by the cells, thus placing them again in a state of irritability.

The following statements are according to the explanation given by SACHS, and have special reference to the petiole of the *Mimosa*-leaf.

1. The motile organ is supplied with two tissue-cushions: the *lower* cushion is *irritable*, the upper cushion causes the movements.

2. There is a high tension in the succulent parenchyma of the two cushions; in this condition they are said to be balanced. In the irritable state there is also tension, but the tension between upper cushion and vascular bundle is greater than the tension between lower cushion and vascular bundle.

3. The decrease in volume in the lower cushion is due to the escape of water from its cells, externally noticeable by a darker coloration. The water escapes in part into the intercellular spaces of the upper cushion, in part into the tissue of the stem and a small portion into the vascular bundle.

Behavior of Tendrils. Conduction of Stimuli. The Function of Irritable Movements.

In tendrils there is an irritable movement induced by contact (not by shock) associated with processes of growth. This irritability is usually not general, but limited to one side of the organ. *Growth is always reduced in the side irritated.* As a result, the tendril lying in contact with some support, curves toward that support by a process of circumnutation; this brings other portions of the tendril in contact with the support, the stimulus is transmitted along the line of contact, finally causing the entire free portion of the tendril to wind about the support in the form of a spiral. The stimulus is also continued toward the basal portion of the tendril (continued from the point of contact above), which cannot come in contact with the support. The stimulus (support) causes the formations of the curvatures or windings. The support and the tendril or climbing plant are drawn toward each other; that is, the tendril has a tendency to form coils whose radii of curvature are less than that of the support, provided the support is not too slender nor the tendril too thick. Besides these windings due to contact there are produced *turning-points*, or places where the direction of the coil changes. There may be one or several of these changes, and they always occur in the free portion of the tendril, that is, in the portion between the support and the stem of the plant. The origin of such coils is due to a mechanical cause, and may be very readily illustrated as follows: A narrow stretched strip of india-rubber is firmly cemented along another strip of rubber not stretched. Upon releasing the tension of the former rubber, it contracts and forms the inside of a spiral, the outer side of which is formed by the strip that was not stretched. Tendrils without a support usually coil slowly in the form of a spiral, but *without* the formation of turning-points.

According to DE VRIES, the first effect of the contact-stimulus is to increase the turgor of the side not stimulated. (For particulars see the text-books of SACHS and PFEFFER.)

Careful studies of irritability have been made by the DARWINS (father and son), later also by WIESNER, DETLEFSEN, HABERLANDT, and others. According to Haberlandt, the irritable stimulus in *Mimosa* is propagated along a system of special stimulus-conducting cells which have highly permeable plasmic membranes (pore-membranes) along the transverse septæ. These special cells lie either within or along the outside of the leptome-bundle. The permeable membranes allow the ready passage of water-currents, which are supposed to be the cause of the irritable movements.

The propagation of stimuli in tendrils is but little understood; also the propagation of stimuli causing geotropic and hydrotropic curvatures. Opinions differ even in regard to the observed facts of the geotropic curvatures of roots. I will briefly state the results of KRABBE'S investigations, which have verified the observations made by CISIELSKIS and DARWIN.

The sensible or irritable portion of the root-tip is never more than 2 mm. long. The portion of the root which is really capable of curving is not wholly located in the 2 mm. of the root-tip. Cutting off 2 mm. from the root-tip does not prevent the root from continuing its growth. Accordingly Darwin concludes that the root-tip receives a stimulus from the force of gravity and transmits it to the zone of maximum growth. Of course it is not implied that the root possesses a "conscious" power to transmit this stimulus. SACHS maintains, moreover, that shoots behave differently; they curve geotropically even when the entire apex is removed. (According to DARWIN, root-tips undergo circumnutation; this is denied by SACHS.)

In regard to the utility of irritable movements due to shock and contact we will state the following: In the case of tendrils this utility is very evident, for by such irritable movements they are enabled to function as organs of adhesion and support. The irritable movements of the stamens of *Cynareæ* are described and explained as follows. A visiting insect causes the stimulus by coming in contact with the anther, which thereby suddenly contracts the anther-tube, while the hair-like bristles of the style which is not irritable "brushes" out some of the pollen, which is carried away by the insect to fertilize another plant. In regard to *Mimosa*, SACHS made the observation that this plant is able to withstand hail much better than more robust plants, because the very first contact suffices to place it in the irritated position; that is, the leaflets become folded and the petiole sinks. PFEFFER supposes that such movements also serve as a protection by frightening away animals. Among "insectivorous" plants the irritable organs serve to catch insects, as has been explained in the case of *Drosera*.

E. THE PHYSIOLOGY OF TWINING.

One of the most complicated phenomena in the plant-creation is the *twining of plants*. It is not an irritable movement in the narrower sense, produced by shock and contact. Here we find combined with circumnutation the effect of negative geotropism and the influence of apparent and real torsion.

It is well known that the stem of a climbing plant (as hops, beans, *Calystegia*, *Ipomœa*, etc.) winds about a support in the form of a spiral. The mechanics of this process is essentially different from that of the winding of tendrils. To understand it well it is necessary for the investigator to have special preparation in mechanics and mathematics. The study of this problem was begun by von Mohl and Palm, and continued by Charles Darwin and H. de Vries. Great advances in this study have recently been made by the investigations of Schwendener, Baranetzky, and Ambronn. The following explanation is based upon the results of Ambronn's and Schwendener's investigations.

The active factors in twining are (1) circumnutation of the growing stem-apex and the resistance of the support; (2) negative geotropism. Both factors aid each other in their effects. Circumnutation makes seizure of or contact with the support possible; subsequently it is necessary that the *contact-stimulus* should continue upward and that the *curvature* should be continuous for a time at least. The advancing of the contact-point is induced by the return pressure of the support. The support exerts a radial pressure outward against the point of contact behind α (Fig. 171), which necessarily increases and extends the contact area at β. Antidromic torsions prevent a stem-portion as at γ, which must become somewhat elongated on the side facing the support due to the pressure of the support, from elongating equally on the outer side when it comes into the position β. Negative geotropism causes the horizontally or diagonally placed apical stem-portion to curve upward and again brings it in contact with the support at some point higher up, when the effects of the pressure will again come into play, as has just been explained. Negative geotropism also assists in another way in forming permanent spirals. It causes curvatures by the more active growth of a continuous tissue-portion which describes a homodromic spiral line around the stem.

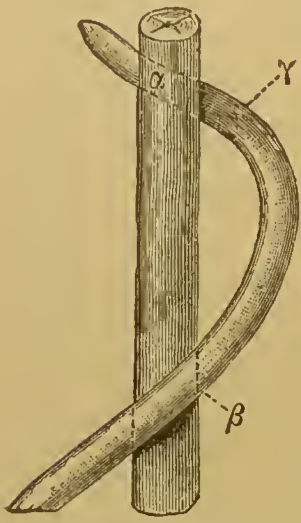

Fig. 171.

We have yet to mention the influence of apparent[1] and real torsion in the process of twining. According to Ambronn and Schwendener, apparent torsion causes spiral curvatures, which hasten or favor the twining about the support. The amount of true antidromic torsion influences in a high degree the mobility of the internodes, so that the amplitude of the movements of nutation decreases with the increase of antidromic torsion. (Within certain limits the amount of true torsion increases as the thickness of the support increases. Apparent torsion increases with the closeness of the spirals.)

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[1] An apparent torsion may be represented by a cylindrical staff cut into many sections, fastened together by spirally-arranged hinge-joints, which are wound about some support. In the case of twining true torsions are caused by the lateral pressure of the support acting upon a diagonal portion of the stem. (See Fig. 171.)

SCHWENDENER has demonstrated that by eliminating the weight of the overhanging stem-apex twining is not in any way disturbed, which proves that the weight of the plant is not an essential factor in the process of twining.

PART VI.

CLASSIFICATION OF PLANTS. TAXONOMY.

A system of classification is said to be *artificial* when it is based upon limited but constant characters. A system is said to be *natural* when it is based upon all the characters of the organism. Usually, however, the idea of "natural descent" is associated with a natural system. It is supposed that descent is the cause of the resemblance or similarity of the plants or other organisms. It is generally admitted that the natural system which is to be the expression of natural origin and descent is being gradually discovered, hence does not yet actually exist. It is customary at present to consider the natural system[1] as directly opposed to the system of LINNÉ.[2] Nevertheless the system of Linné as well as the various natural systems are at the same time natural and artificial.

Many of the plant-families of the so-called natural systems coincide more or less with the classes or orders of Linné's system.[3] The following table will illustrate this more clearly.

The families given at the right harmonize with the following classes and orders of Linné:

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[1] A. L. DE JUSSIEU is usually credited with having introduced the natural system of plants.—TRANS.

[2] See p. 288 for Linné's Classification.

[3] Acherson, Flora der Provinz Brandenburg.

III. Class		Gramineæ.
V. “	1. Order	Primulaceæ.
V. “	“	Boraginaceæ.
V. “	“	Solanaceæ.
V. “	1. and 2. Order	Gentianaceæ.
V. “	2. Order	Umbelliferæ.
V. “	“	Chenopodiaceæ.
VI. “		Liliifloræ (in part).
XII. “		Rosaceæ.
XIII. “	1. Order	Papaveraceæ.
XIII. “	2. and 3. Order	Ranunculaceæ.
XIV. “	1. Order	Labiatæ.
XV. “		Cruciferæ.
XVI. and XVII. Class		Papilionaceæ.
XIX. Class		Compositæ.
XX. “		Orchidaceæ.
XXI. “		Cupuliferæ.
XXI. “		Coniferæ.

That Linné's system of phanerogams is artificial is evident from the fact that it includes the *Coniferæ* and *Cupuliferæ* in one and the same class. He has also combined the *Umbelliferæ*, *Boraginaceæ*, *Solanaceæ*, etc.

Nevertheless the system of Linné is in part *natural* and in part *artificial*. This is true of all phanerogamic systems, hence also of every system which is said to be *natural* as opposed to the system of Linné. The impartial scientist[1] may well question the value of the much-praised naturalness of the natural systems. I say natural *systems*, because there are a large number of them. It is wholly out of the question at the present time to consider *all of the characteristics* in the arrangement of plants. The essentials of these natural systems are based upon the characters of the flower and the fruit.

The value of anatomical characters has long been proven. These characters have, however, only been applied within narrow limits. It has even been supposed that comparative anatomy would sooner or later come in serious conflict with the present natural systems. I do not believe, that comparative

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[1] Compare Schwendener's Rectoratsrede, Berlin, 1887.

The Classes of Linné's System (SEUBERT).

Phanerogams	Perfect flowers (bisexual)	Stamens and pistils not united	Stamens free	Stamens of equal length	Stamens, as to number	1 stamen	I. Monandria.
						2 stamens	II. Diandria.
						3 “	III. Triandria.
						4 “	IV. Tetrandria.
						5 “	V. Pentandria.
						6 “	VI. Hexandria.
						7 “	VII. Heptandria.
						8 “	VIII. Octandria.
						9 “	IX. Enneandria.
						10 “	X. Decandria
						12–19 “	XI. Dodecandria.
					Stamens, as to number and position	20 and more stamens upon the corolla	XII. Icosandria.
						20 and more stamens upon the torus	XIII. Polyandria.
				Stamens of unequal length	Two long and two short		XIV. Didynamia.
					Four long and two short		XV. Tetradynamia.
			Stamens united	Filaments united	In one bundle		XVI. Monodelphia.
					In two bundles		XVII. Diadelphia.
					In several bundles		XVIII. Polyadelphia.
				Anthers united			XIX. Syngenesia.
		Stamens united with the pistils					XX. Gynandria.
	Unisexual flowers (dicliny)	Staminate and pistillate flowers on the same plant					XXI. Monœcia.
		“ “ “ “ “ different plants					XXII. Diœcia.
		Staminate, pistillate, and perfect flowers on the same plant					XXIII. Polygamia.
Cryptogams							XXIV. Cryptogamia.

anatomy will ever aid in establishing a natural system of the various dicotyledonous groups, based upon descent, because such a system is not possible. We may, no doubt, succeed in arranging certain groups upon definite anatomical characters. These characters are, however, useless when applied to other groups. Again, it will be found that the selection of other anatomical characters will lead to a different arrangement. The reason that we cannot find a system which would also represent a phylogenetic tree lies in the absence of a natural descent, and not in the lost or hidden branches of this tree. The bond which unites the organisms of a kingdom is a *spiritual* one, it is the *uniform Creative Idea.* A phylogenetic relationship, if it exists at all, is very limited.

In conclusion I will give the plant-system of EICHLER.[1]

A. Cryptogamæ.

- I. DIVISION : THALLOPHYTÆ.
  - *I. Class : Algæ.*
    - I. Group : Cyanophyceæ.
    - II. " Diatomeæ.
    - III. " Chlorophyceæ.
      - 1. Series : Conjugatæ ; 2. series : Zoosporeæ ; 3. series : Characeæ.
    - IV. Group : Phæophyceæ.
    - V. " Rhodophyceæ.
  - *II. Class : Fungi.*
    - I. Group : Schizomycetes.
    - II. " Eumycetes.
      - 1. Series : Phycomycetes ; 2. series : Ustilagineæ ; 3. series : Æcidiomycetes ; 4. series : Ascomycetes ; 5. series : Basidiomycetes.
    - III. Group : Lichenes.
- II. DIVISION : BRYOPHYTA.
    - I. Group : Hepaticæ.
    - II. " Musci.
- III. DIVISION : PTERIDOPHYTA.
  - *I. Class : Equisetinæ.*
  - *II. " Lycopodinæ.*
  - *III. " Filicinæ.*

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[1] Syllabus, 1886.

B. Phanerogamæ.

I. DIVISION: GYMNOSPERMÆ.

II. " ANGIOSPERMÆ.

I. Class: Monocotyleæ.

1. Series: Liliifloræ; 2. series: Enantioblastæ; 3. series: Spadicifloræ; 4. series: Glumifloræ; 5. series: Scitamineæ; 6. series: Gynandræ; 7. series: Helobiæ.

II. Class: Dicotyleæ.

I. Subclass: Choripetalæ.

1. Series: Amentaceæ; 2. series: Urticinæ; 3. series: Polygoninæ; 4. series: Centrospermæ; 5. series: Polycarpicæ; 6. series: Rhoeadinæ; 7. series: Cistifloræ; 8. series: Columniferæ; 9. series: Gruinales; 10. series: Terebinthinæ; 11. series: Æsculinæ; 12. series: Frangulinæ; 13. series: Tricoccæ; 14. series: Umbellifloræ; 15. series: Saxifraginæ; 16. series: Opuntinæ; 17. series: Passiflorinæ; 18. series: Myrtifloræ; 19. series: Thymelinæ; 20. series: Rosifloræ; 21. series: Leguminosæ; appendix: Hysterophyta.

II. Subclass: Sympetalæ.

1. Series: Bicornes; 2. series: Primulinæ; 3. series: Diospyrinæ; 4. series: Contortæ; 5. series: Tubifloræ; 6. series: Labiatifloræ; 7. series: Campanulinæ; 8. series: Rubiinæ; 9. series: Aggregatæ.

ENGLER[1] divides the monocotyledons into ten series. The *Palmæ, Pandanales, Spathifloræ,* and *Synanthæ* are treated as special series. He also subdivides the *Choripetalæ* more than does Eichler. Both authors almost agree in the arrangement of the *Sympetalæ.* Engler treats the *Plantaginales* as a distinct series.

Finally, we will refer to Nägeli's system of classification. This investigator was especially anxious to establish a natural system, but he could not decide whether the monocotyledons or the dicotyledons constituted the most highly organized group of plants. He was, however, inclined to consider the monocotyledons as the higher group. This author maintains that certain families have become extinct, and therefore the phylogenetic connection is no longer directly visible. Should this connection be visible we would find, according to Nägeli, the lower uniting branches of the phylogenetic tree ; these lower branches have become extinct. All this assumption is pure speculation. It is not probable that a system of natural descent will ever be established. Since Nägeli desires to establish such a system, he must *assume* the original existence of such extinct plant-groups, of which even palæontology reveals no record.

---

[1] Guide to the Royal Botanical Garden of the University at Breslau, 1886.

Natural in the sense of *according to nature* (not in the sense of according to a natural descent) is that arrangement of plants which proceeds from simpler forms to those more complicated. We may also say that the arrangement of series from "lower" to "higher" is natural ; but not from "imperfect" to "perfect." (It would be wrong and meaningless to say an alga is imperfect because it lacks vascular bundles ; the algæ do not require such organs.) The arrangement of plants into cellular plants and vascular plants, into cryptogams and phanerogams, into thallophytes and cormophytes (plants with stems and leaves), seems according to nature. Not any observed facts of a natural descent, but our reasoning faculty, leads us to make such classifications. It is a spiritual bond which unites all organisms. This bond is the *Idea* of the *Creator*.

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